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NAME OF AUTHOR/*NOM DE L'AUTEUR* Jack C. Mauer

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NAME OF SUPERVISOR/*NOM DU DIRECTEUR DE THÈSE* Dr. J. M. Mayo & K.E. Denford

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COMPARATIVE ECOPHYSIOLOGY OF THE CHROMOSOME RACES IN VIOLA ADUNCA J.E. SMITH

by

JACK C. MAUER

(C)

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE

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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Comparative Ecophysiology of the Chromosome Races in Viola adunca, J.E. Smith" submitted by Jack C. Mauer in partial fulfilment of the requirements for the degree of Master of Science.

James M. Mayo

Supervisors

Lawrence C. Bliss

Kenneth Higginbotham

Date December 16, 1976

ABSTRACT

Plants from diploid and polyploid populations of Viola adunca from the Cypress Hills, Alberta were compared physiologically in terms of light and temperature responses of net assimilation, dark respiration; and the responses of water potential, relative water content, leaf resistance and net assimilation to desiccation. Investigations were carried out in order to determine if polyploid plants performed differently than diploid plants and to determine if polyploidy per se conferred any greater hardiness. It was hoped the investigation would explain distributional differences of the different populations. Single attached leaves of polyploid V. adunca had maximum net assimilation rates of 26 mg CO_2 g^{-1} hr^{-1} (12 mg CO_2 dm^{-2} hr^{-1}) while diploid rates were 23 mg CO_2 g^{-1} hr^{-1} (11 mg CO_2 dm^{-2} hr^{-1}) at 20° C and 500 μEm^{-2} sec^{-1} light intensity. The net assimilation responses at very low and high temperatures were quite similar for both ploidy levels. There were no statistically significant differences in the light compensation, light saturation or 1/2 saturation values over the temperature interval from 0 to 40° C. Dark respiration rates of polyploid V. adunca were 2.2 mg CO_2 g^{-1} hr^{-1} (1.0 mg CO_2 dm^{-2} hr^{-1}) and diploid rates were 2.0 mg CO_2 g^{-1} hr^{-1} (0.95 mg CO_2 dm^{-2} hr^{-1}) at 20° C. The mean maximum water potential of both ploidy levels was -7.9 bars. Minimum leaf resistance remained near 3.6 sec cm^{-1} for both ploidy levels and net assimilation attained maximum rates at water potential of -9 bars until

a threshold water potential of -14 bars was reached. The data leads to the conclusion that polyploid and diploid V. adunca are almost identical physiologically and that polyploid plants are not hardier than diploid plants with respect to the parameters studied.

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INTRODUCTION

It is well established in the taxonomic literature that the polyploids of a species are usually more widely distributed, i.e., found in more severe environments than diploids of the same species (Cain, 1944; Löve and Löve, 1949; Stebbins, 1950; and Johnson, Packer and Reese, 1965). Löve and Löve (1943) studied the chromosome numbers of the European flora and accumulated evidence suggesting that the incidence of polyploidy in a flora increases with increasing latitutde. They further postulated that polyploids are hardier than their diploid ancestors, i.e, more resistant to cold. Gustafsson (1946) was critical of this theory as he thought that correlations between polyploidy and latitude were highly complex and that the "inferences on polyploidy superiority must be taken with great caution." Hagerup (1933) and Muntzing (1936) showed that chromosome races often differ ecologically as well as geographically. Early transplanting experiments (Clausen, Keck and Hiesey, 1945; and Bowden, 1940) of ecological races and different ploidy levels indicated that the theory of greater tolerance of polyploids to environmental parameters is questionable, compared to their diploid counterparts. That is, diploids and polyploids did not separate along environmental parameters.

Polyploidy has also been strongly associated with historical events of specific regions, e.g., glacial history (Stebbins, 1971; and Johnson, Packer and Reese, 1965). Work done at Ogotoruk Creek in Alaska showed that the percentage of polyploidy is related to the

effects of glaciation and the polyploids seemed to be favored in the most recently disturbed habitats (Johnson and Packer, 1965). The physiological mechanisms which may help explain these observed geographical and ecological differences for a given species consisting of chromosome races are virtually lacking.

Viola adunca, J.E. Smith is a widely distributed North American perennial herb ranging from the prairies to lower alpine regions. Three known chromosome races exist in this complex; 2N = 20, 2N = 30 and 2N = 40. The triploid V. adunca is relatively rare and thought to have arisen from crosses between tetraploid and diploids (McPherson, 1972). Polyploidy in V. adunca is thought to be a case of autopolyploidy (McPherson, 1972; and Gershey, 1934). The tetraploids have a more northerly distribution than the diploids although in Alberta all three chromosome races are found in the Cypress Hills, an area thought to have been a glacial refugium during the last ice age (see Figure 1 after McPherson, 1972).

The purpose of this study was to compare selected physiologic responses of the chromosome races of V. adunca from optimal moisture and temperature conditions to stress levels through measurements of: 1) net carbon dioxide assimilation (N.A.), 2) dark respiration, 3) water potential and its components, and 4) leaf diffusion resistance. These experiments should show if there are any physiological differences between chromosome races and if polyploid plants have a greater amplitude of environmental tolerances than the diploids of the same species. It should also show whether polyploidy per se confers any greater tolerance to a broader range of environmental conditions.

Figure 1. Distribution map of the chromosome races of Viola adunca in Alberta after McPherson (1972).

MATERIALS AND METHODS

Growing Regime

Viola adunca plants were collected from the Cypress Hills of southeastern Alberta during the spring of 1975. The specimens were dug up with their roots intact and transferred to plastic pots in their native soil and marked according to site. In Edmonton the plants were removed from their native soil and planted in standard greenhouse potting soil composed of the following mixture: 3 parts loam, 2 parts peat, and 2 parts sand. The plants were grown in the greenhouse under the following conditions: day/night temperatures 20° and 16° C respectfully, relative humidity was 50%, natural lighting conditions were used in summer, and in winter artificial lights consisting of a mixture of multivapor and lucalux bulbs were used to maintain a 15 hour photoperiod. Plants were fertilized with a mixture of 20-20-20 NPK fertilizer at the start of the growing season. Plants remained active for ca. 6 - 8 weeks after which time they started to senesce, requiring a rest period. Plants also became infested with red spider mite (*Tetranychus bimaculatus*) from time to time. Dormancy was induced by gradually lowering the temperature from 18° to -2° C over an 11 day period. At the same time the photoperiod was reduced from ca. 15 hours to 7 horus. The plants were then stored for two weeks at -2° C in the dark. After this treatment and a thorough spraying with Lindane to kill spider mite eggs the plants could be induced into a

vigorus growing condition by putting them directly into their growing regime (defined above). The plants did well under these conditions, and plants from both ploidy levels flowered twice during the growing season.

Determination of Ploidy Level

A. Guard Cell measurements

Previous work indicated that the different ploidy levels of Viola adunca were quite similar morphologically speaking, i.e., no gross size differences between chromosome races were noted by McPherson (1972). Stomatal length of V. adunca has been positively correlated with ploidy level (McPherson, 1972). Measurements of guard cell lengths were made on leaf epidermal peels of the adaxial surface. Peels were taken from live material by simply stripping the leaf epidermis off with a pair of fine tipped forceps. The peels were mounted in water and stomata measured using a graduated eyepiece fitted to a Vickers microscope (Vienna). Twenty-five guard cells were measured from each of the 60 specimens. The guard cells of tetraploid specimens averaged ca. 31.5 microns (μ) (±4μ) while diploid specimens averaged ca. 25.5 μ(±4μ).

B. Chromosome counts

Root tips were taken from the plants after the plants had established themselves in pots. Excised root tips were treated with a 0.002 M solution of 8-hydroxyquinoline (0.016 gm in 400 ml of water)

for three to four hours at 14° C (±2° C) (Tjio and Levan, 1950). This solution halts mitosis at metaphase, leaving the shortened and thickened chromosomes attached to the metaphase plate. The root tips were then washed in distilled water for five minutes and transferred to the staining solution of 9 parts acetic orcein to 1 part 1N HCL in a watch glass. The root tips and solution were then warmed over a bunsen burner 3 to 6 times during a 15 minute period. Finally the root tips were placed in a drop of 45% acetic acid on a slide and squashed between it and a cover slip. The squashing procedure spreads the cells, and disrupts the metaphase plate, leading to dispersal of the chromosome complement throughout each cell. Semipermanent mounts were made by applying a mixture of Canada balsam and melted paraffin around the edges of the cover slip. Chromosome numbers were then counted using a Zeiss microscope (Oberkochen, West Germany) with green filters under a magnification of 400 x .1. The chromosome numbers of 23 plants were treated in this fashion and their ploidy levels determined.

Carbon Dioxide Exchange

A. Equipment and General Method

In these experiments, the net assimilation rates were assumed to be the net rate of uptake or efflux of CO_2 by the attached leaf in question (Šesták, Catský and Jarvis, 1971). Since photosynthesis and respiration will be occurring in the tissue at the same time, net

assimilation can be defined as that difference between gross photosynthesis and respiration.

The rates of net assimilation of the plants in question were determined by enclosing a single attached leaf of each individual under investigation into an open gas analysis system (Šesták, Catský and Jarvis, 1971). To facilitate ease of comparison between ploidy levels, and to increase accuracy, two cuvettes were utilized. The attached leaves of two ploidy levels would thus receive approximately the same light, temperature, and humidity conditions throughout an experiment. Carbon dioxide uptake or efflux was measured differentially with an UNOR II infra-red gas analyzer (IRGA) (Mahik, Hamburg) spanned 35 ppm full scale and calibrated with standard gases as described by Bate, D'Aoust and Canvin (1969). Terostat VII (Terosan, Heidelburg) was used to seal the leaves into the cuvettes around the petiole. Diagrams of cuvettes used and a flow chart of the analysis system used are to be found in Appendix A.

Leaf temperature in the cuvettes was controlled by adjusting the temperature of the entire growth chamber. The temperature of the air and leaves inside, as well as outside of the cuvettes were monitored continuously with 0.003 inch copper-constantan thermocouples (Omega Engineering, Stamford, Conn.). Both the IRGA and thermocouple outputs were recorded continuously with a Honeywell (Electronik 16) 24 channel multipoint stripchart recorder with a built-in electronic reference junction for the thermocouples.

Illumination was provided by standard chamber lighting consisting

of a mixture of 100 watt incandescent and warm white flourescent lamps supplemented by either a tungsten-halogen lamp (Sylvannia Corp.) controlled by a variable autotransformer or a Mercury Vapor Lamp (General Electric).

Illumination was also achieved by using a high illumination chamber without any accessory lighting (Environmental Growth Chamber, Chagrin Falls, Ohio). The lighting in this special chamber consists of a mixture of multivapor, lucalux and incandescent lamps. Desired illumination levels were thus achieved in different ways depending on the chamber and light source being utilized. In the case of the mercury vapor lamp, the distance between the cuvette and lamp were changed, and in the case of the tungsten-halogen lamp, a rheostat (the variable autotransformer) was utilized to achieve the desired intensity. When the high illumination chamber was used a combination of lamps were utilized to achieve the intensity required. Spectral analyses for all lamps are listed in Appendix B (page 84).

Photosynthetically active radiation (PAR 400-700 nm) was measured with a quantum sensor in microensteins per square meter per second ($\mu E.m^{-2}.s^{-1}$) and illuminence was measured in lux; both sensors were supplied by Lambda Instruments (Lincoln, Nebraska) with meter no. L1-185. Spectral analysis was made on the various lighting fixtures with an ISCO spectroradiometer (Instrumental Specialities Co., Lincoln, Nebraska). The effects of light and temperature on the net assimilation rates were studied as outlined in Table 1.

B. The Effect of Light Intensity and Temperature on Net Assimilation

The response of net assimilation to light intensity was examined by maintaining the leaves at a constant temperature and changing the incoming radiation every 1.5 hours. The light response was examined at five leaf temperatures in the following fashion: temperatures of 0°, 10°, 20°, 30° and 40° C were held constant while the light intensity was varied through the following sequence 800, 500, 400, 300, 200, 100, 50, ca. compensation (25-7) μEm^{-2} sec^{-1} and, dark.

The direct effect of temperature on net assimilation was determined by subjecting the leaves to ranges of temperature; 45° to 0° C in 5° steps for 1.5 hours each. (A preliminary measurement was made at 20° C so that any adverse high temperature effects could be recognized.) High temperatures may adversely effect certain enzymes and chloroplast structures, as evidenced by slowing down the rates of net assimilation for a considerable time after lowering of the temperature (Larcher, 1969). Dark respiration was examined for 15 minutes at the end of each temperature step.

C. The Effect of Soil Drying on Net Assimilation

The response of net assimilation to decreasing soil moisture was examined by maintaining the leaf at a constant temperature and light intensity. (Net assimilation and dark respiration rates were measured every 24 hours as the soil moisture content decreased, i.e., soil water potential (ψ) became more negative.) For further detail see water relations technique.

Table 1. General experimental conditions for measuring net assimilation response to leaf temperature, light intensity and moisture stress.

Type of Experiment	Light Condition	Dark Condition	Leaf Temperature °C	Time for Each Condition	Air Flow Rate (ml min^{-1})	Order of Changing Environmental Parameters	Time for one experiment
Direct temperature response	Constant 500 μEm^{-2} s^{-1} PAR 300 μEm^{-2} s^{-1} PAR	15 min. at end of each temperature step	varied in 5° steps	1 hr	140	warm to cold and cold to warm	16 hrs
Light response	varied	15 min at end of experiment	constant at selected temperature	1 hr	140	high light to low light	8 hrs
Net assimilation response to moisture stress	500 μEm^{-2} s^{-1} PAR	15 min at end of experiment	20°	1 hr	140	drying	6 days

D. Calculations for Gas Exchange Data

At the end of the experiment the leaves were harvested to determine their leaf area and dry weight. Leaves were first traced on graph paper and the area determined by counting the number of squares enclosed within the leaf trace for one leaf surface only. Then the leaves were oven dried at 70° overnight and weighed on an analytical balance (Mettler H10, Zurich). Net assimilation rates are thus calculated on the basis of milligrams CO_2 assimilated per gram dry weight per hour (mg g^{-1} hr^{-1}) and milligrams CO_2 assimilated per decimeter^2 leaf area per hour (mg dm^{-2} hr^{-1}) according to equation 1 after Hargerink (1975).

1) Net Assimilation of CO_2 (mg g^{-1} hr^{-1}) or (mg dm^{-2} hr^{-1}) =

$$(Cppm \times Y \frac{mg}{mlppm} \times \frac{273}{T_1 °K} \times F \frac{ml}{min} \times 60 \frac{min}{hr}) \div \text{either } W_1 g^1 \text{ or L.A. } dm^2$$

Where: C = amount of CO_2 assimilated in ppm

Y = conversion from ppm to mg ml^{-1}

$$= \frac{44 \times 10^{-6}}{22.414} \text{ mg } ml^{-1} \text{ } ppm^{-1}$$

T_1 = leaf temperature in °K

F = flow rate of air through the cuvette in ml min^{-1}

W_1 = dry weight of leaf in grams

L.A. = leaf area of one surface in decimeter.^{2}

The system was designed with two cuvettes so that comparisons between both ploidy levels could be made during the same experiment. A cam switching device was used to switch the air streams between the

two cuvettes each containing a single leaf. The following switching sequence was used: cuvette I for 30 minutes, reference air 15 minutes, cuvette II for 30 minutes. In this manner two plants of different ploidy levels were studied at the same time.

The means of the net assimilation rates and the confidence intervals at the 95% confidence level were plotted against the light intensity or temperature used, to attain light response and temperature response curves.

Because the magnitude of net assimilation approaches an asymptote (called the light saturation point) in response to increasing light intensity, this light saturation point is not clearly defined. This had led to difficulties in comparing the light response information presented by other authors (Hartgerink, 1975). Since the shape of a light response curve is a hyperbolic curve, the values of light intensity required to bring about a rate of net assimilation equal to one-half of the projected maximum rate (P_{50}) at each temperature have been calculated, according to equation 2 used in enzyme kinetics to describe a parabolic function (Rabinowitch and Govindjee, 1969; Lehninger, 1970).

2) $$V = \frac{Vmax\ [S]}{Km + [S]}$$

Where: V = net assimilation rate

Vmax = maximum net assimilation rate

Km = constant

S = light intensity

NOTE: The Km constant is equal to the light intensity at which the net assimilation rate is half maximal and can be obtained by plotting the inverse of the net assimilation rate vs the inverse of the light intensity. The result is a straight line from which the Km value is taken at the X-axis intercept.

Light saturation was defined after Hartgerink (1975) as that light intensity at which a 100% increase in irradiance would yield no more than a 10% increase in the net assimilation rate. This was done in order to compare results with other light saturation values reported in the literature.

Water Relations Experimental Methods

A. Psychrometers

Spanner-type psychrometers were used to measure both total water potentials (ψ) and component water potentials (ψ_p and ψ_γ, equation 3). The psychrometers were constructed after Mayo (1974). Psychrometers were calibrated with NaCl solutions of known water potential in a constant temperature water bath. Output was measured with a Fluke model 845-AB high impedence microvoltmeter. The psychrometer sample chambers were 4 mm in diameter and 6 mm in depth. Each sample consisted to 2 uniform size leaf discs, 6 mm in diameter cut from the leaves with a paper punch. Total leaf water potential was determined first, then the chambers and samples were wrapped tightly in aluminum foil and placed in liquid nitrogen (-196° C) for 10 minutes. This

ruptures the cell membranes and thus eliminates the turgor component (ψ_p) of the leaf water potential. After the liquid nitrogen treatment, samples and chambers were thawed to room temperature using a heat gun for a few minutes and then put back into the psychrometers for measurement of the combined osmotic and matric components. In this fashion an estimate of the original turgor pressure was calcualted from equation 3.

3) $\psi = \psi_p + (\psi_\pi + \psi_\gamma)$

and $\psi_p = \psi - (\psi_\pi + \psi_\gamma)$

Where: ψ_p = turgor pressure

ψ = total water potential

$|\psi_\pi + \psi_\gamma|$ = combined osmotic and matric components

B. Water Potential, Leaf Resistance, Relative Water Content and Net Assimilation as Related to Moisture Stress

Well-watered plants from both ploidy levels in an actively growing condition were allowed to dry out in a controlled environment chamber. The temperature was kept at 20° C and the relative humidity (R.H.) close to 75 - 80%, with 15 hours of lighting under 200-250 $\mu E\ m^{-2}\ sec^{-1}$ PAR (10,000 lux, irradiance), during the course of these experiments except where otherwise noted. Daily measurements of the water potential and component water potentials as well as leaf resistance net assimilation and dark respiration rates, and relative water content were made on fully mature leaves until the plants wilted.

1. Leaf Resistance

Leaf resistances were measured directly with a Diffusive Resistance Meter model LI-60 (Lambda Corp., Lincoln, Nebraska) on both abaxial and adaxial leaf surfaces since V. adunca is amphistomatous. The sensor was calibrated with a resistance plate which has pores of known resistance (drilled holes to simulate leaf resistance) (Kanemasu, Thurtell and Tanner, 1969). The total leaf resistance (R_L) was calculated from equation 4 after Nobel (1974).

4) $$\frac{1}{R_L} = \frac{1}{R_{AB}} + \frac{1}{R_{AD}}$$

Where: R_{AB} = leaf resistance abaxial surface

R_{AD} = leaf resistance adaxial surface.

2. Relative Water Content

The relative water content (RWC) was determined on mature fully expanded leaves after Slavik (1974). The leaf discs were removed using a paper punch and weighed directly after removal from the leaf to determine fresh weight. The discs were then allowed to inhibe distilled water at room temperature for 3 1/2 hours in a polyfoam lined petri-dish (with individual holes for each disc) and weighed again to determine a weight turgid. Finally the discs were oven dried overnight to 70° C to obtain their dry weight. The relative water content was obtained using equation 5, after Slavik (1974).

5) $$RWC = \frac{\text{weight fresh - weight dry}}{\text{weight turgid - weight dry}} \times 100.$$

Net assimilation rates were measured at 20° C leaf temperatures and at 500 μEm^{-2} sec^{-1} PAR. Dark respiration rates were also measured for a half-hour each. The number of replicates for each individual experiment for each ploidy level is shown in Table 2.

Table 2. Number of experimental replicates made during the investigation.

Type of Experiment	Number of Replicates	
	2n	polyploid
Light response at each temperature (°C)		
0°	8	10
10°	8	10
20°	18	11
30°	8	10
40°	8	5
Temperature response at each light intensity (μEm^{-2} sec^{-1})		
300	5	5
500	4	4
Drying response at constant light and temperature	4	4

THE EFFECT OF LIGHT INTENSITY ON NET ASSIMILATION

Literature Review

Light intensity is an important environmental parameter which can influence the species composition existing at a given time in an ecosystem. For example, changes in understory composition have been recorded in deciduous forests in response to tree canopy closure, with early species being replaced by more shade tolerant species (Vezina and Grandtner, 1965; Jackson, 1966). Species present before canopy closure may undergo changes in their photosynthetic mechanisms which enable them to utilize increasingly lower light levels during and after canopy closure (Sparling, 1967; Taylor and Pearcy, 1976).

The effect of light intensity on net assimilation has been studied for a wide variety of species; Böhning and Burnside (1956), Sparling (1967), Taylor and Pearcy (1976), have studied the light response characteristics of temperate herbaceous and agricultural plants. Larcher (1969) has reviewed the literature for trees, and Hartgerink (1975) has reviewed the literature for arctic and alpine plants. The general effect of light intensity on net assimilation has been reviewed by Hesketh and Moss (1963), Hesketh and Baker (1967), and Rabinowitch and Govindgee (1969). Considerable variation in the response pattern of net assimilation to light intensity exists, the basis for which is understood to be biochemical (Mooney, 1972). Because this variation is due to the carbon dioxide fixation pathway plants can be classified according to the nature of the pathway. The first plant group discussed is

called C_4 plants because they possess the dicarboxylic acid pathway in which the initial photosynthetic product upon carboxylation is a 4-carbon carboxylic acid. These plants are characterized by remarkably high absolute net assimilation rates (up to 70 mg dm^{-2} hr^{-1}, see Table 3), net assimilation rates not fully saturated at full sun light, a very high temperature optimum for photosynthesis, and are efficient water users (Berry, 1975; Mooney, 1972). The second group of plants discussed is called the C_3 plants because a 3-carbon phosphorylated acid is the initial product of carboxylation in their photosynthetic mechanism. These plants are characterized by lower absolute net assimilation rates (4-30 mg dm^{-3} hr^{-1}, see Table 3), a lower temperature optimum for net assimilation, fully saturated net assimilation rates at lower light intensities, and have lower water use efficiency per gram of dry matter obtained (Böhning and Burnside, 1956; Šesták, Catský and Jarvis, 1971; Mooney, 1972). The C_3 plants can be further classified into sun and shade plants. Sun plants possess higher absolute net assimilation rates, light saturation and compensation points than shade plants (Böhning and Burnside, 1956; Sparling, 1967; Taylor and Pearcy, 1976). The distinctions between sun and shade plants are not always clear as in many cases intermediates between a 'true' sun plant and shade plant exist based on their light response characteristics. For example, Sparling (1967) made intermediate categories for some of the plants he studied from the woodlands of Ontario in his comparative light response survey of a number of species.

Comparative studies of the light response characteristics between ecotypes and varieties of the same species have been described. Basic

Table 3. Light compensation and saturation points, and net assimilation rates of various plant groups at optimum temperature.

Origin	Compensation Point (ft-c)	Saturation Point (ft-c)	Net Assimilation Rate (mg dm^{-2} hr^{-1})	Reference
Arctic and Alpine	150-300	$\leq$5000		Hartgerink, 1975
Temperate C_3				
Sun	50-220	1000-3000	10-30	Sparling, 1967: Böhning and Burnside, 1956; Sěsták, et al., 1971
Shade	50	1000	4-16	
Temperate C_4	+300	$\geq$8000	30-70	Berry, 1975; Sěsták, et al., 1971
Conifers	150-300	3000-5000	4-12	Larcher, 1969; Sěsták, et al., 1971

photosynthetic differences have been found to exist between ecotypes of Solidago virgaria (Björkman and Holmgren, 1963) native to habitats with differing light intensities. Similar results were found in Atriplex glabriuscula (Björkman and Holmgren, 1966). These differences are the same as those described for sun and shade plants (page 19). The shade races possess a lower carboxylating enzyme content than do the sun races and this is thought to be the underlying difference between races (Berry, 1975). Eickmeir, Adams, and Lester (1975) found that southern populations of Tsuga canadensis had greater absolute net assimilation rates and greater efficiency of net assimilation at low irradience levels than northern populations. The northern populations had greater dark respiration rates which probably helped to explain these differences.

The available data from comparative studies on the light responses characteristics of chromosome races of a species is meager as most studies of this nature usually concentrated on the absolute net assimilation rates at one temperature. The net assimilation rates and photosynthetic light efficiency (meaning greater percentage of maximum net assimilation at a given light intensity) of polyploid arctic Thalictrum alpinum was found to be only slightly greater than for arctic diploids collected from the same area (Mooney and Johnson, 1965). Photosynthetic studies on Hippocrepis comosa L. has shown the tetraploids of this species show a greater photosynthetic light efficiency as well as possess greater absolute net assimilation rates than the diploids (Guenn, Bourdu and Roux, 1975). The absolute net assimilation rates in polyploids are however, usually reported to be lower than for

those in diploids as observed in Hordeum vulgare (Ekdahl, 1944); Ribes (Bjurman, 1959); Vitis vinifera (Geisler, 1961); Raphanus sativus (Frydrych, 1965); and Brassica oleracea var. gorgyloides (Frydrych, 1965). The results from many of these studies must be viewed with caution since the researchers sometimes used only one plant from each ploidy level, and the experimental conditions varied tremendously with each study, making comparisons difficult.

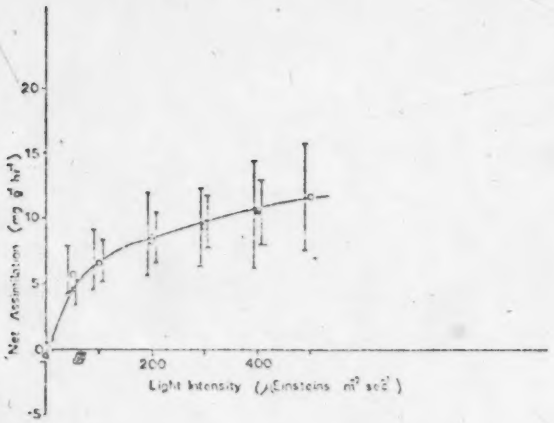
Results and Discussion

The responses of net assimilation of the ploidy levels in Viola adunca to light intensity at five leaf temperatures is shown in Figures 2, 3, 4, 5 and 6. The manner in which net assimilation was expressed had an effect upon the comparisons. For example, at 20° C the diploids had greater absolute net assimilation rates and slightly greater photosynthetic variability as shown by the confidence intervals when expressed on a mg dm^{-2} hr^{-1} basis (Figure 4b, page 28). When expressed as mg g^{-1} hr^{-1} however (Figure 4a), it is the polyploids which show greater net assimilation rates and photosynthetic variability. These differences are not statistically significant as indicated by the similar absolute net assimilation rates and overlapping confidence intervals. At 30° C the diploids again show greater net assimilation rates and photosynthetic variability when expressed on a mg dm^{-2} hr^{-1} basis (Figure 5b, page 27) but on a mg m^{-1} hr^{-1} basis (Figure 5a) these differences are much less pronounced. The manner in which net assimilation was expressed had little effect upon the comparisons at 0°, 10° and 40° C (Figure 2,

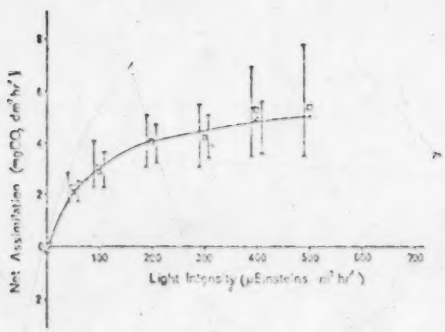
3 and 6). At 0° and 40° C the absolute net assimilation rates at each experimental light level used are virtually identical, but the polyploids exhibited greater variability of photosynthesis as shown by the confidence intervals (Figures 2a, 2b, 3a and 3b). The light response at 10° C (Figure 3, page 26) shows that the tetraploids have greater absolute net assimilation rates at almost each experimental light level as well as greater photosynthetic variability.

To summarize briefly, in three out of five temperatures used in the response of net assimilation to light intensity, polyploids exhibited a greater photosynthetic variability, and at one temperature, greater rates of net assimilation. Diploid plants exhibited greater variability of net assimilation rates at two of the temperatures used, but the manner in which net assimilation was expressed modified these results. One can conclude from these results that some differences between ploidy levels exist, but considering the overlapping confidence intervals and considerable number of samples taken these differences are not statistically significant. It is important that ploidy level differences at extremely low (0° C) and high (40° C) temperatures were not statistically significant, therefore polyploids do not exhibit any greater tolerance to the extremes studied.

There were no significant differences in the light compensation and saturation points or the 1/2V max values (P_{50}) (Figures 2, 3, 4, 5 and 6), and because of this the light response data at various leaf temperatures have been combined for both ploidy levels, summarized in Table 5 (page 37). As leaf temperatures were increased from 0° to 40° C there was an exponential increase in the light compensation

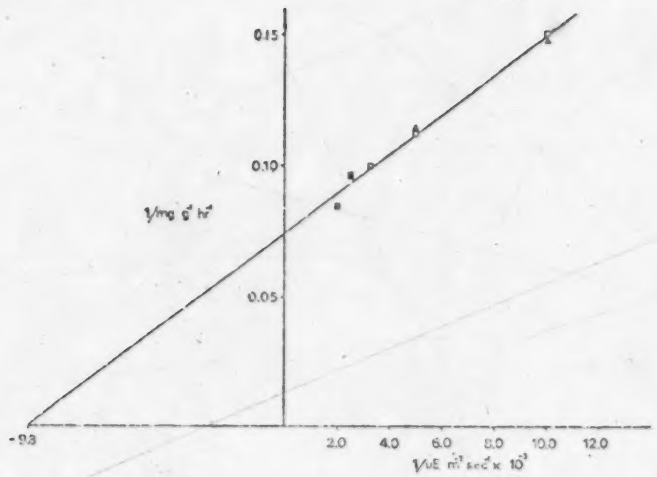


a) Net assimilation on a mg CO_2 g^{-1} hr^{-1} basis vs. light intenstiy.

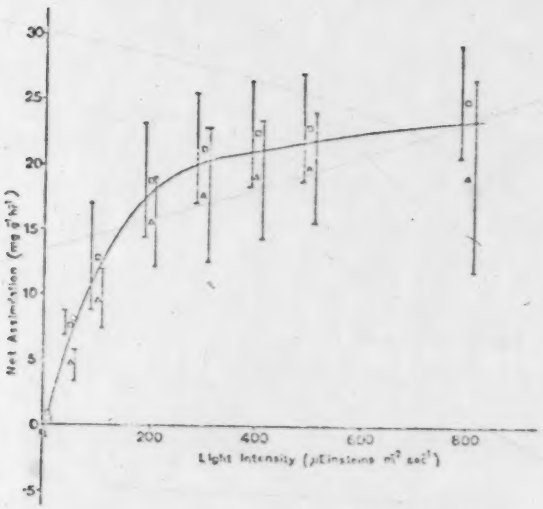


b) Net assimilation on a mg CO_2 dm^{-2} hr^{-1} basis vs. light intensity.

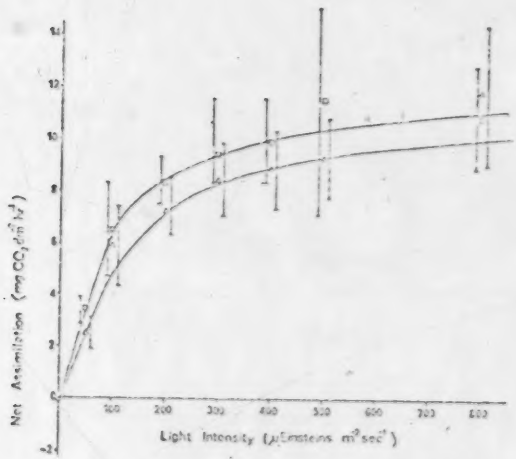
Figure 2. The response of net assimilation by single attached leaves of the chromosome races in Viola adunca at 0° C.
(□--3n and 4n plants, and △--2n plants)



c) Lineweaver-Burke plot of $\frac{1}{\text{N.A.}}$ vs. $\frac{1}{\text{Light Intensity}}$ to define 1/2 saturation (P_{50}) values.

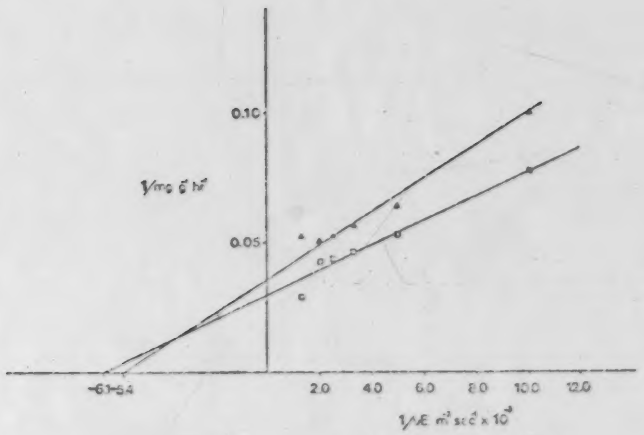


a) Net assimilation on a mg CO_2 g^{-1} hr^{-1} basis vs. light intensity.

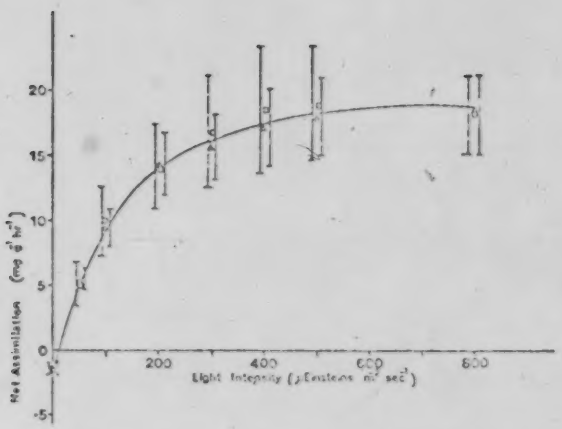


b) Net assimilation on a mg CO_2 dm^{-2} hr^{-1} basis vs. light intensity.

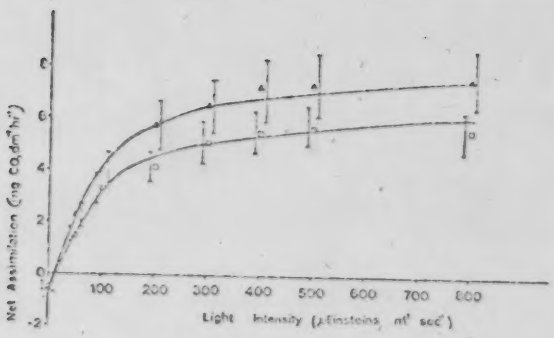
Figure 3. The response of net assimilation by single attached leaves of the chromosome races in Viola adunca at 10° C.
(□ --3n and 4n plants, and △ --2n plants)



c) Lineweaver-Burke plot of $\frac{1}{N.A.}$ vs. $\frac{1}{\text{Light Intensity}}$ to define 1/2 saturation (P_{50}) values.

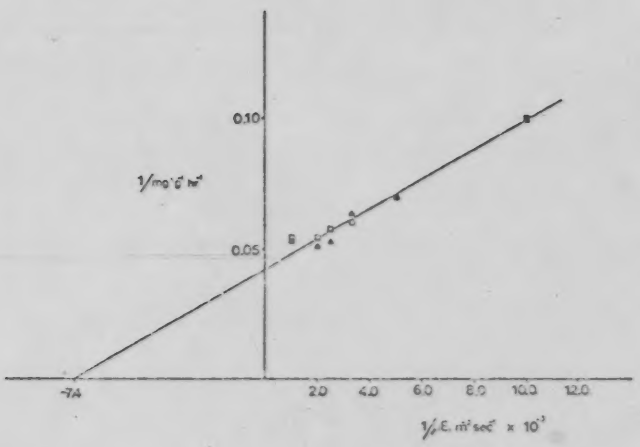


a) Net assimilation on a mg CO_2 g^{-1} hr^{-1} basis vs. light intensity.

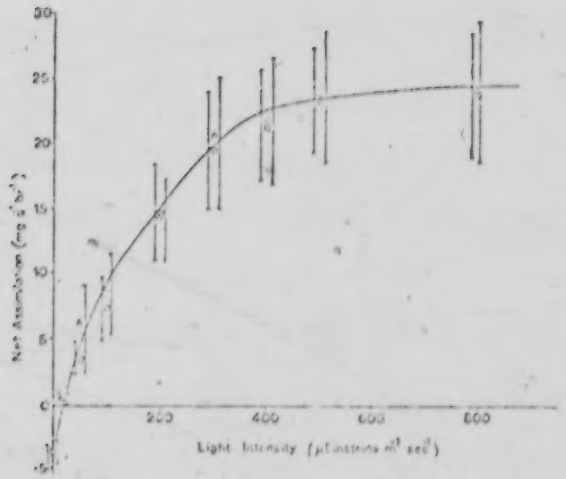


b) Net assimilation on a mg CO_2 dm^{-2} hr^{-1} basis vs. light intensity.

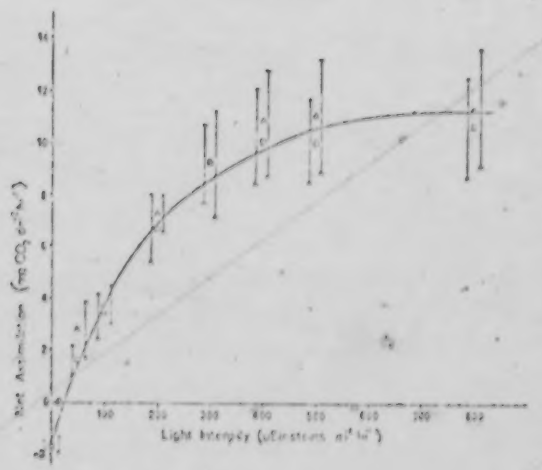
Figure 4. The response of net assimilation by single attached leaves of the chromosome races in Viola adunca at 20° C.
(I□--3n and 4n plants, and △I--2n plants)



c) Lineweaver-Burke plot of $\frac{1}{\text{N.A.}}$ vs. $\frac{1}{\text{Light Intensity}}$ to define 1/2 saturation (P_{50}) values.

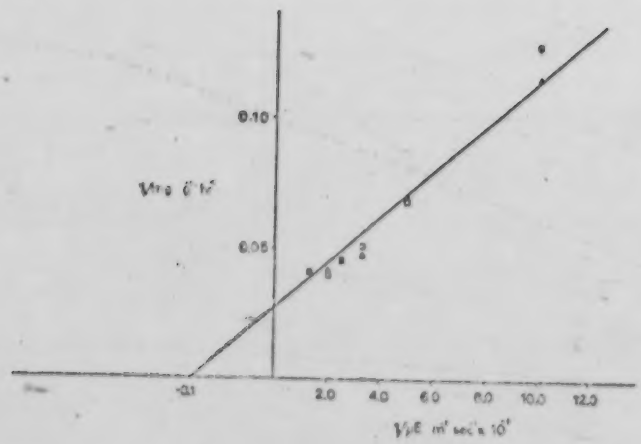


a) Net assimilation on a mg CO_2 g^{-1} hr^{-1} basis vs. light intensity.

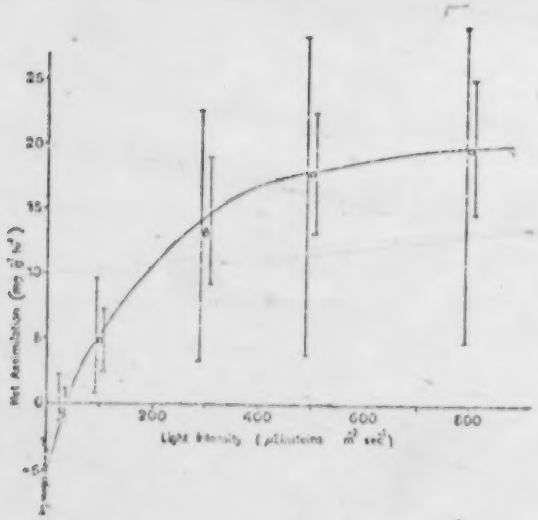


b) Net assimilation on a mg CO_2 dm^{-2} hr^{-1} basis vs. light intensity.

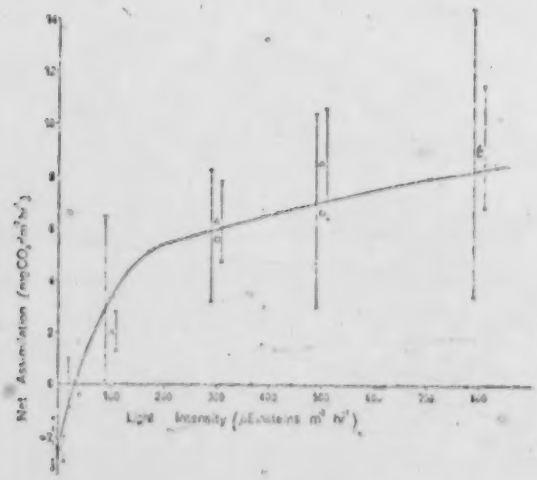
Figure 5. The response of net assimilation by single attached leaves of the chromosome races in Viola adunca at 30° C.
(I□--3n and 4n plants, and △I--2n plants)



c) Lineweaver-Burke plot of $\frac{1}{\text{N.A.}}$ vs. $\frac{1}{\text{Light Intensity}}$ to define 1/2 saturation (P_{50}) values.

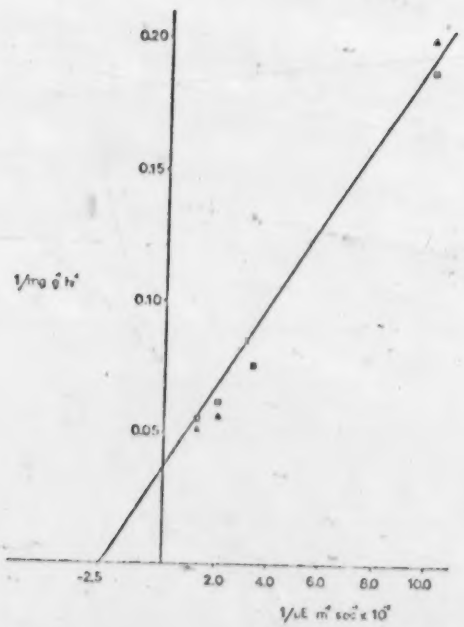


a) Net assimilation on a mg CO_2 g^{-1} hr^{-1} basis vs. light intensity.



b) Net assimilation on a mg CO_2 dm^{-2} hr^{-1} basis vs. light intensity.

Figure 6. The response of net assimilation by single attached leaves of the chromosome races in Viola adunca at 40° C.
([□ --3n and 4n plants, and △--2n plants)



c) Lineweaver-Burke plot of $\frac{1}{\text{N.A.}}$ vs. $\frac{1}{\text{Light Intensity}}$ to define 1/2 saturation (P_{50}) values.

point as well as significant, but nonexponential, increases in the dark respiration rate over the same temperature interval (Figure 7, page 35). The dark respiration rate increase is the probable cause for the light compensation point increase (Rabinowitch, 1956; Larcher, 1969; Hartgerink, 1975). It may be that the rate of photorespiration also increased over this temperature interval which would further explain the increasing light compensation point. Photorespiration however, usually has the same temperature optimum for net assimilation which may rule out this possibility (Hofstra and Hesketh, 1969).

The light intensities at which net assimilation of V. adunca approaches saturation and 1/2 saturation (P_{50}) at 5 leaf temperatures are listed in Table 5. These values increase in a nonexponential fashion. In this respect, these results are similar to those found by Hartgerink (1975) for Dryas integrifolia. The light saturation point at 20° C (2,400 ft-c) is in the upper range for temperate C_3 sun plants, yet the light compensation point at this temperature (60 ft-c) is in the lower range for plants of this category (Table 3, page 20). Thus V. adunca is able to utilize effectively a wide range of light levels and in this respect is very similar to Erythronium americanum (Table 4, page 36) which is also a spring ephemeral (Sparling, 1967). V. adunca is quite unlike other species of violets listed in Table 4 (V. sororia and V. pubescens) which possess lower light compensation and saturation points and are thus more like true shade plants (Sparling, 1967).

The P_{50} values of Viola adunca at 20° C (1160 ft-c) are much higher than for those reported for such shade tolerant species as

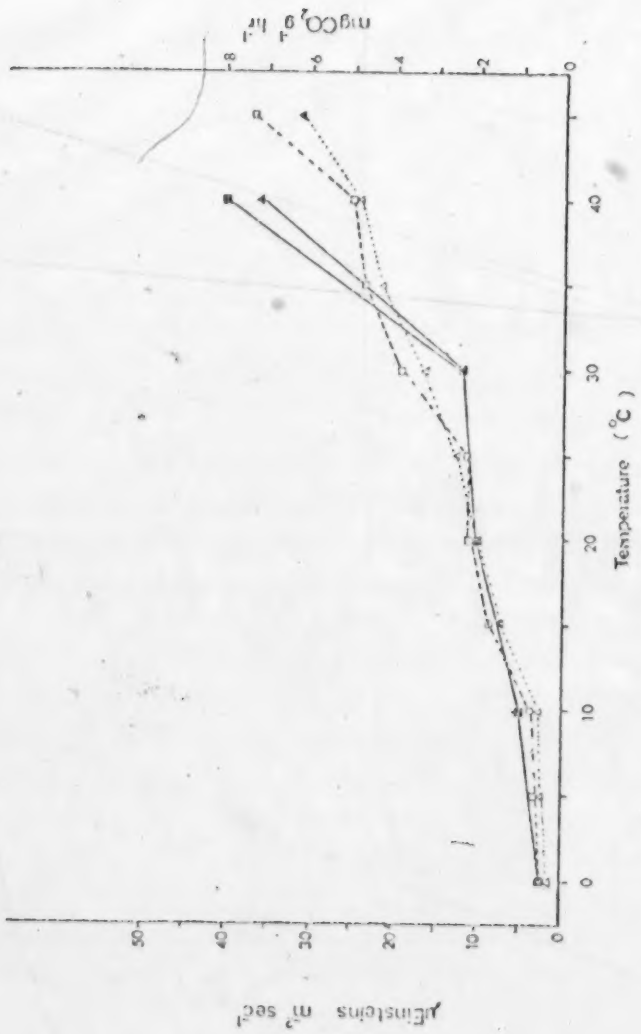


Figure 7. Light compensation points (solid lines) and dark respiration rates (2n plants dotted lines, 3n and 4n plants dashed lines) of Viola adunca leaves.
(■ and □ polyploid, ▲ and △ diploid)

Table 4. Temperate sun and shade plant light response characteristics at 25° C.

Plant	Light Compensation (ft-c)	Light Saturation (ft-c)	Reference
Dicentra candensis	150-222	3000	Sparling, 1967
Claytonia caroliniana	180	1500	Sparling, 1967
Caulophyllum thalictroides	70-130	3000	Sparling, 1967
Erythronium americanam	45-84	3000	Sparling, 1967
Viola adunca	66	2400	This Study
Viola sororia	40	300	Sparling, 1967
Viola pubescens	32	350-1000	Sparling, 1967
Dryopteris	50	500	Böhning and Burnside, 1956
Oxalis	70	1000	Böhning and Burnside, 1956
Trillium erectum	50-60	250	Sparling, 1967

Table 5. Light compensation, saturation, and 1/2 saturation points of *Viola adunca* at various leaf temperatures. Combined data for both ploidy levels.

Temperature °C	Compensation Point ft-c μEm^{-2} sec^{-1}*		Saturation Point ft-c μEm^{-2} sec^{-1}*		1/2 Saturation (P_{50}) ft-c μEm^{-2} sec^{-1}*	
0°	18	3	1200	200	670	111
10°	30	5	1800	300	1100	182
20°	60	10	2400	400	1160	192
30°	72	12	2400	400	1930	320
40°	228	38	3000	500	2400	400

*Light intensities measured in 400 to 700 mm range (PAR).

Sassafras albidum (600) (Bazzaz, Paape and Boggess, 1972), Acer rubrum (750), Fagus grandifolia (500) and Quercus velutina (750) (from Bazzaz, Paape and Boggess, 1972, as calculated from Loach, 1967 data). The P_{50} values of V. adunca are slightly higher than for such shade intolerant species as Liriodendron tulipifera (900) and Populus tremuloides (1000) (from Bazzaz, Paape and Boggess, 1972, as calculated from Loach, 1967 data). This information combined with low light compensation point (Table 4) and moderately high light saturation point suggest that V. adunca has unique light response characteristics.

It should be noted that the absolute net assimilation rates at 20° C (Figure 4) are lower (for both ploidy levels) than at either 10° C or 30° C (Figure 3 and 5) even though 20° C is optimum temperature for net assimilation (see pages 45 and 49). The light response runs at 20° C were made on plants which had not undergone a period of dormancy (see Page 4) following initial establishment in their pots. All subsequent runs at 0°, 10°, 30° and 40° C were made on plants which did have a dormancy period. It appears that V. adunca requires a period of dormancy in order to attain its maximum spring-time net assimilation rates and that this dormancy period is genetically determined. Similar findings were made by Hartgerink (1975), Addison (pers. comm., 1975), Bourdeau (1959), Parker (1961) and Bamberg, Schwarz and Tranquillini, (1971).

THE EFFECT OF TEMPERATURE ON NET ASSIMILATION AND DARK RESPIRATION

Literature Review

Temperature is an important environmental factor (parameter) controlling net assimilation under natural conditions. It is postulated that the reason why polyploid races of a species are found growing farther north than diploid counterparts is that polyploids are "hardier" than diploid counterparts (page 1) (Löve and Löve, 1971; Löve and Löve, 1974). Thus if polyploid species are "hardier" than diploids they are likely to be able to assimilate CO_2 more efficiently at lower leaf temperatures than diploids. The effect of temperature on the net assimilation rates of the chromosome rates in V. adunca was examined to: 1) determine if polyploids are more efficient at assimilating CO_2 over a wider temperature range than diploid counterparts, 2) to establish if there are any differences in the temperature optimum for net assimilation, and 3) to compare the upper and lower limits for compensating gas exchange and dark respiration between ploidy levels.

Net assimilation rates follow a well known optimum curve around a favorable temperature range (Hesketh and Baker, 1967) and the shape of this curve is species variable. The net assimilation rates of temperate C_3 plants show an optimum temperature response between 10° - 35° C (Murata and Iyama, 1963; Hofstra and Hesketh, 1969) and usually the shape of the temperature response curve shows a broad plateau around the temperature optimum (Hofstra and Hesketh, 1969). This broad plateau is

postulated by Zelitch (1971) to be due to parallel increases in the photorespiration rate following the same temperature optimum as photosynthesis (e.g., Hartgerink, 1975). In contrast to this, C_4 plants have a higher temperature optimum for net assimilation above or below which they show preciptuous decreases with temperature (Hofstra and Hesketh, 1969; Berry, 1975). It must be remembered that C_4 plants do not exhibit photorespiration and thus the narrow temperature optimum C_4 plants exhibit (Hofstra and Hesketh, 1969) may be a function of not having any detectable photorespiration. The temperature optimum for a number of plants of temperate origin are listed in Table 6 (page 50).

Above or below the favorable temperature range, net assimilation becomes smaller until the limits are reached where CO_2 evolution equals uptake (Bauer, Larcher and Walker, 1974). The heat limit or heat compensation point is quite variable and comes very close to the lethal limit for the plant (Levitt, 1972). Furthermore a relationship exists between the heat limit and the type of habitat from which a given plant group is found growing naturally. For example, desert and tropical plants exhibit a higher heat limit than temperate climate plants (Bauer, Larcher and Walker, 1974). On the average, C_4 plants show a higher temperature limit for CO_2 uptake than C_3 plants (Bauer, Larcher and Walker, 1974). This is thought to be due to better carboxylating capacity of phosphoenolpyruvate (PEP) carboxylase at high temperatures found in C_4 plants (Zelitch, 1971) in conjunction with large increases in respiration found in C_3 plants at high leaf temperatures (Hofstra and Hesketh, 1969).

The cold limit for net assimilation can also be considered a compensation point for those plants of warm climate origin in that net

assimilation ceases above the freezing point. This is true in both warm climate dicotyledons and grasses (Ludlow and Wilson, 1971). In contrast to this, plants which are chilling resistant or insensitive (Levitt, 1972) have net assimilation rates which cease at the freezing point of the leaf or assimilating organ. It is not accurate to say that these plants have a cold compensation point since the freezing temperature of the leaf can be several degrees below 0° C (Pisek, Larcher and Unterholzner, 1967). Chilling insensitive plants achieve this degree of cold hardiness by an avoidance mechanism (Levitt, 1972). This mechanism could be a biochemical adaptation of the cell membranes of these plants. For example, Lyons, Wheaton and Pratt (1964) found that plants which are chilling insensitive contained a higher content of polyunsaturated fatty acids in the mitochondrial membranes than in those plants which were chilling sensitive.

The temperature optimum and heat and cold limits are also affected by the acclimation temperature of the growing regime (Mooney and Shropshire, 1967; Billings, et al., 1971; Downton and Slatyer, 1972; Bauer, 1972). That is, the above mentioned gas exchange parameters can be altered in the direction of the acclimation temperature. For example, plants acclimated to a growing regime of 30°/20° C day-night temperatures will usually show higher temperature optimum and heat compensation points than the same plants acclimated to 20°/10° C day-night growing regime (Bauer, Larcher and Walker, 1974). Thus it becomes important when making ecophysiological comparisons to make sure that plants being compared are acclimated to the same growing regime. The acclimation response is not found universally in all plant groups studied.

No detectable acclimation response was found in Dactylis glomerata (Treharne and Eagles, 1970) or in Dryas integrifolia (Hartgerink, 1975).

Dark respiration rates are less sensitive to high temperatures than photosynthesis (Bauer, Huter and Larcher, 1969) and are considered to be one of the most heat stable life functions (Alexandrov, Lomagin and Fielddman, 1970). Dark respiration usually has a Q_{10} of 2 to 3 between 10° and 20° C leaf temperature regardless of the plant group studied (Hartgerink, 1975). There are indications that dark respiration is severely inhibited by light (Benson and Calvin, 1950; Graham and Walker, 1962; Hofstra and Hesketh, 1969; Mangat, Levin and Bidwell, 1974). Thus to achieve a thorough understanding of a leaf carbon balance one must consider that at temperatures close to thermal optimum, photorespiration is reportedly 1.3 to 2 times as great as dark respiration (Hofstra and Hesketh, 1969). At leaf temperatures greater than 40° C the magnitude of the dark respiration rate will however, be greater than the rate of photorespiration (Hofstra and Hesketh, 1969). This is because dark respiration will be increasing exponetially (Larcher, 1969) while photorepiration will be decreasing since it has the same temperature optimum as photosynthesis (page 40).

There are strong correlations between the origin of a plant and the rate of dark respiration. For example, greater dark respiration rates were reported in population of Picea excelsea originating from higher elevations than of valley populations (Pisek and Winkler, 1958) at the same temperature. Populations of Atriplex lentiformis originating from a cooler coastal climate had greater respiration rates than desert populations (Pearcy and Harrison, 1974). Similar observations were made of

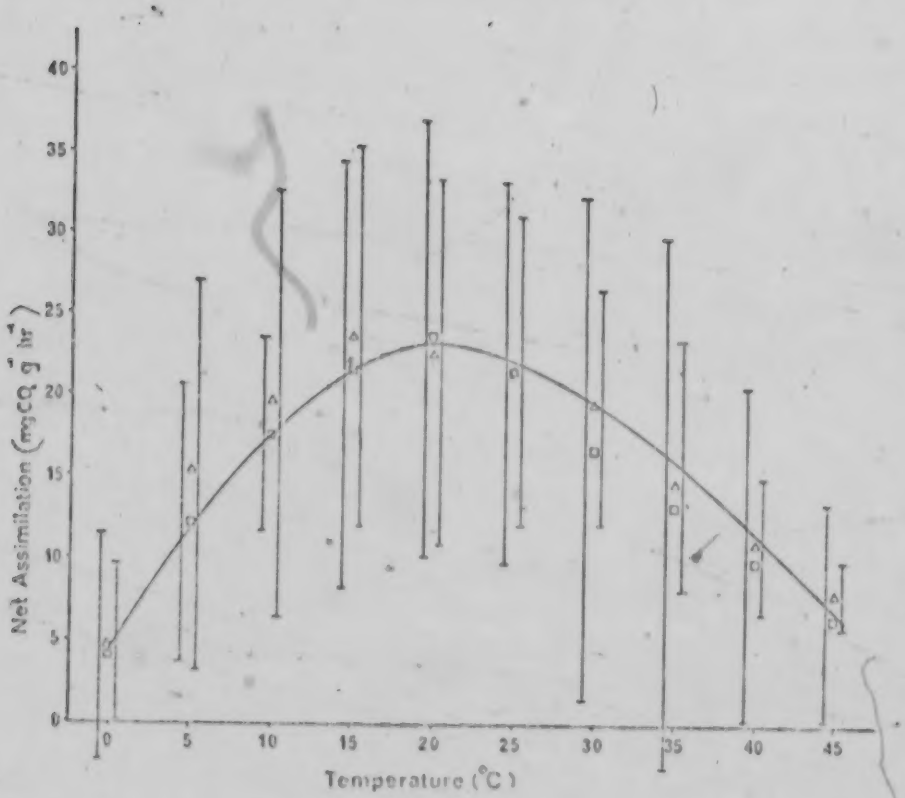
populations of Polygonum bistortoides (Mooney, 1963), Oxyria digyna (Mooney and Billings, 1961) and Tsuga canadensis (Eickmeier, Adams and Lester, 1975). It is thought that the higher rate of respiratory metabolism is an adaptation which would better enable these populations to survive in cooler habitats (Mooney, 1963). However contrary to this, Scholander and Kanwisher (1959) found no difference in respiration rates between southern populations (Massachusetts) of Cladonia spp. Equisetum, Lycopodium, Arenaria, Epilobium, and Campanula vs their northern populations (Labrador).

It is conceivable that if polyploid plants are better adapted to a colder and more northern climatic condition, they may exhibit higher respiration rates than diploid plants as determined in Thalictrum alpinum (Mooney and Johnson, 1965) where 3n and 2n T. alpinum had a dark respiration rate of 5.6 and 4.5 mg CO_2 g^{-1} hr at 20° C. In this study the 3n plants were larger and were more vigorous in appearance than the 2n plants.

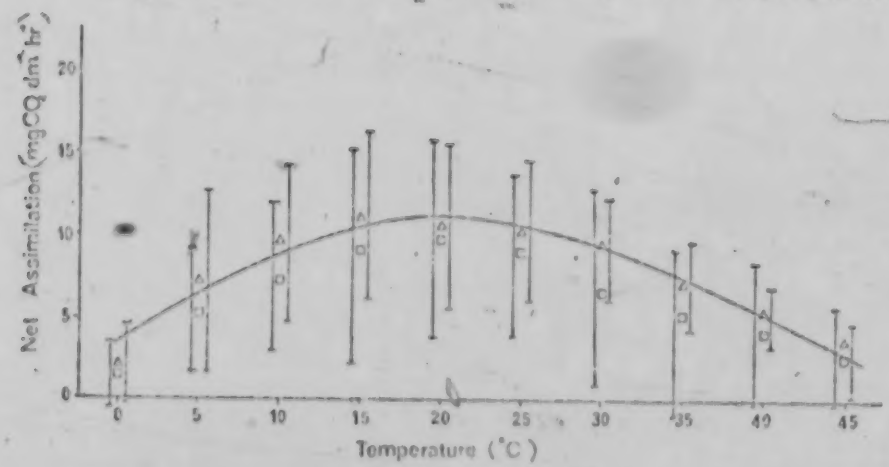
Results and Discussion

The effect of temperature on the net assimilation rates of the chromosome races in Viola adunca is shown in Figures 8, 9, and 10. At a constant light intensity of 300 μE m^{-2} sec^{-1} the diploid plants consistently show greater absolute net assimilation rates (Figures 8a and 8b) (page 45) over the temperature interval from 0° to 45° C. This is true when net assimilation is expressed on a gram weight basis (mg CO_2 g^{-1} hr^{-1}) and a leaf area basis (mg CO_2 dm^{-2} hr^{-1}). The confidence intervals show that there is a slight trend in greater diploid photosynthetic variability at colder temperatures and greater polyploid variability

at warmer temperatures (Figures 8a and 8b). These slight differences between ploidy levels are lessened to an extent however, when net assimilation is expressed as a percent of maximum (Figure 10a) and are not significant. The effect of temperature on net assimilation at a saturating light intensity (page 34) of 500 $\mu E\ m^{-2}\ sec^{-1}$ is shown in Figures 9a, 9b and 10b. At this light intensity it is the polyploid plants which consistently show greater absolute net assimilation rates as well as photosynthetic variability (Figures 9a and 9b). This is evident on both a gram weight and leaf area basis. Since considerable overlap is shown by the confidence intervals, these differences are probably not statistically significant. When net assimilation is expressed as a percentage of maximum (Figure 10b) however, differences are negligible. This indicates that diploid and polyploid plants are as equally efficient at photosynthesis at a given temperature over the range from 0° - 45° C. Variation in the net assimilation rate of both ploidy levels is considerable. This could have been minimized if more samples were used as in the light responses (see Table 2, page 17). Most important, the differences between ploidy levels were slight and generally inconsistent at both light intensities. Because of this, no greater tolerance of polyploid plants is apparent. This is also supported by the fact that plants of both ploidy levels assimilate CO_2 at rates which are reasonably similar at 0° and at 45° C. These extreme temperatures are those which approach the cold and heat limits for net assimilation (page 40). These results contradict those of Mooney and Johnson (1965) who found triploid Thalictrum alpinum had significantly higher absolute net assimilation rates than diploids

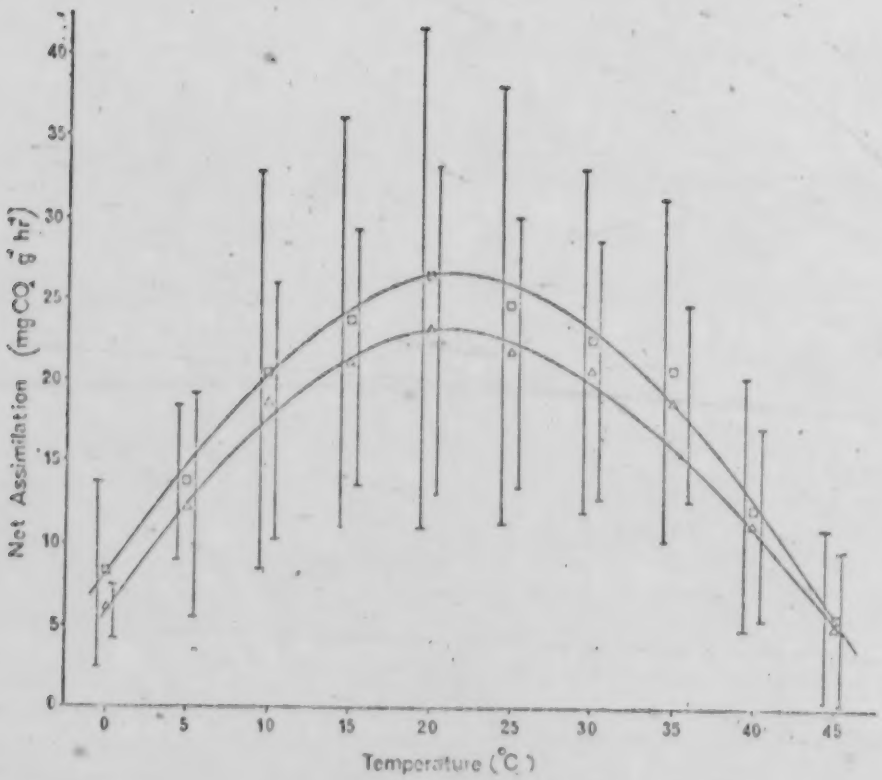


a) Net assimilation on a mg CO_2 g^{-1} hr^{-1} basis vs. temperature.

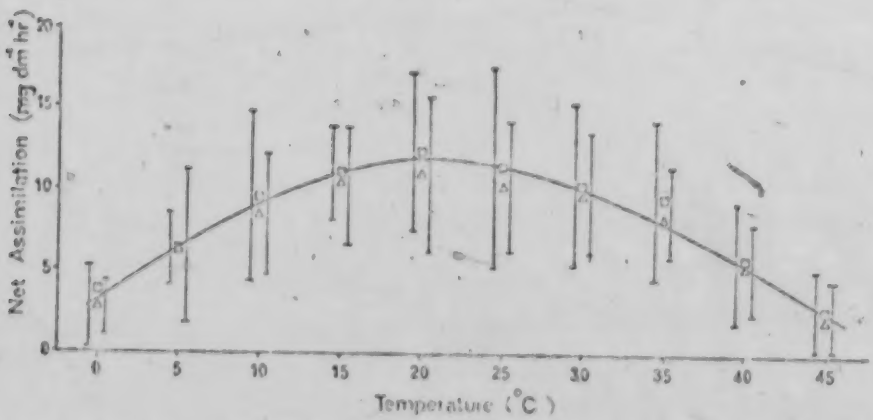


b) Net assimilation on a mg CO_2 dm^{-2} hr^{-1} basis vs. temperature.

Figure 8. The response of net assimilation of the chromosome races in Viola adunca to temperature at 300 μEm^{-2} sec^{-1}. Acclimation temperature 20°C.. (▲--2n plants, □-- 3n and 4n plants)

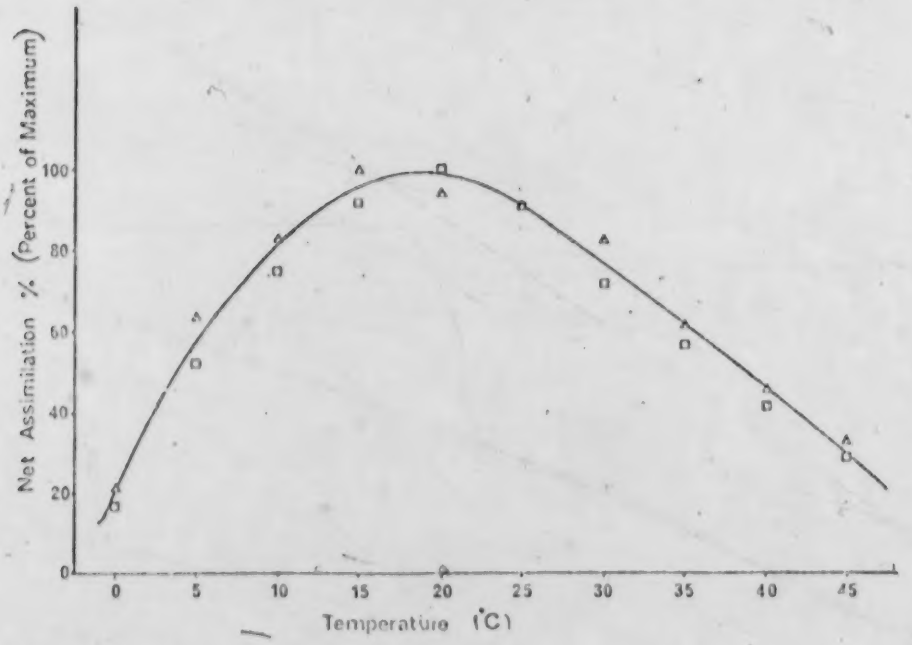


a) Net assimilation on a mg CO_2 g^{-1} hr^{-1} basis vs. temperature.

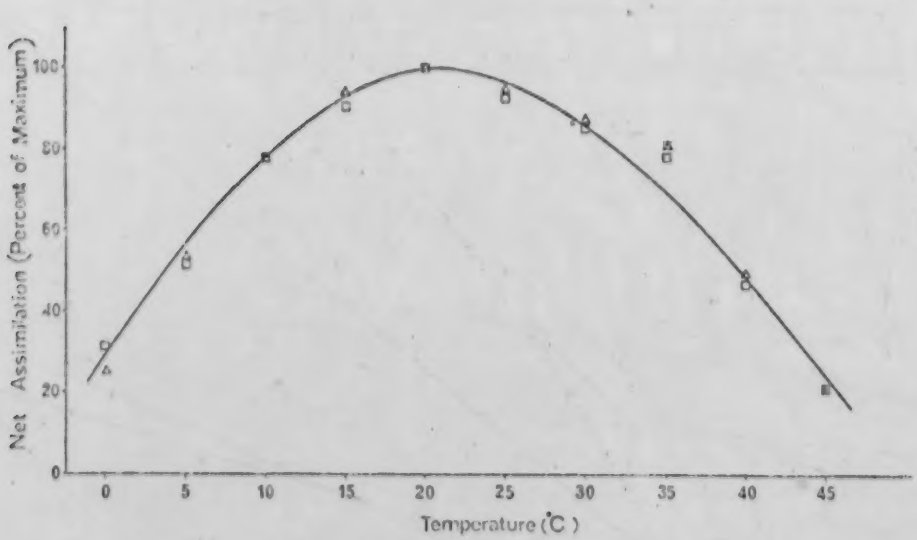


b) Net assimilation on a mg CO_2 dm^{-2} hr^{-1} basis vs. temperature.

Figure 9: The response of net assimilation of the chromosome races in Viola adunca to temperature at 500 μEm^{-2} sec^{-1}. Acclimation temperature 20°C. (▲--2n plants, △-- 3n and 4n plants)



a) Net assimilation vs. temperature at contant light intensity 300 μEm^{-2} sec^{-1}.



b) Net assimilation vs. temperature at constant light intensity 500 μEm^{-2} sec^{-1}.

Figure 10. Response of net assimilation expressed as a percentage of maximum by single attached leaves of Viola adunca to temperature. Acclimation temperature 20°C. (□ --3n and 4n plants, Δ--2n plants)

over a temperature interval from 10°- 30° C. The trend in temperature response for Thalictrum was for greater ploidy differences at higher temperatures than at low temperatures (ca. 17.5 vs 7.5 mg CO_2 g^{-1} hr^{-1} 3n and 2n plants at 30° C respectively while at 10° C rates were 17 vs 13.5 mg CO_2 g^{-1} hr^{-1} 3n and 2n plants respectively). It was noted in the literature review (page 43) that 3n arctic T. alpinum was more vigorous and larger than 2n plants. No such size differences were found between ploidy levels of V. adunca (see page 5).

The data from the net assimilation responses of single leaves of Viola adunca does show that this plant has a considerable degree of thermal tolerance. This is demonstrated not only by the plant's ability to assimilate CO_2 at 0° C and 45° C (Figures 8, 9 and 10), but also by the ability to carry out net assimilation at sub-freezing temperatures. When growth chamber malfunctions created unwanted low leaf temperatures it was discovered that V. adunca can assimilate CO_2 as low as -3° C before leaves freeze and net assimilation stops. Similar findings have been reported in the literature (page 41). The fact that freezing of the leaves occurs at temperatures below 0° C suggests that V. adunca makes use of an avoidance mechanism of frost hardiness (page 41). The ability to assimilate CO_2 over such a wide temperature interval is an important adaptation of V. adunca which enables it to maintain populations in a climate such as the Cypress Hills where spring-time weather can be quite unpredictable. Near freezing night temperatures can be coupled with very warm daytime temperatures in this region (pers. obs.).

The thermal optimum for net assimilation for Viola plants of both ploidy levels is very close to 20° C. The optimum is similar to other temperate herbaceous and arborescent species listed in Table 6 (page 50). Most C_3 plants have their thermal optimum between 15° and 20° C (Larcher, 1969). Also considering 20° C was the daytime growing regime temperature (page 41) it is not surprising that V. adunca had a thermal optimum at 20° C, since plants have been found to acclimate to the temperature of a given growing regime (see literature review, page 41). The average rate of net assimilation at saturating light intensity (500 $\mu E\ m^{-2}\ sec^{-1}$) and optimum temperature for Viola adunca is listed in Table 6. The net assimilation rates are comparable to other native species such as Diospyros virginiana, Ulmus alata and Thalictrum alpinum (Table 6). The rates are much lower than for those of crop plants such as Glycine max and Beta vulgaris (Table 6).

The shape of the temperature response curve of V. adunca is very symmetrical around the thermal optimum (Figures 8, 9 and 10). Decreases in net assimilation at high temperatures are not any sharper than at low temperatures. These results are different for many of the C_3 species examined by Hofstra and Hesketh (1969) who found sharper increases in net assimilation at higher than at lower leaf temperatures. The results for V. adunca are similar to those found in Ulmus alata (Bacone, Bazzaz and Boggess, 1976) and Juniperus virginiana (Ormsbee, Bazzaz and Boggess, 1976) whose temperature response curves are very symmetrical around the thermal optimum.

The effect of temperature on dark respiration rates is shown in Figures 11a and 11b (page 53). Dark respiration rate differences

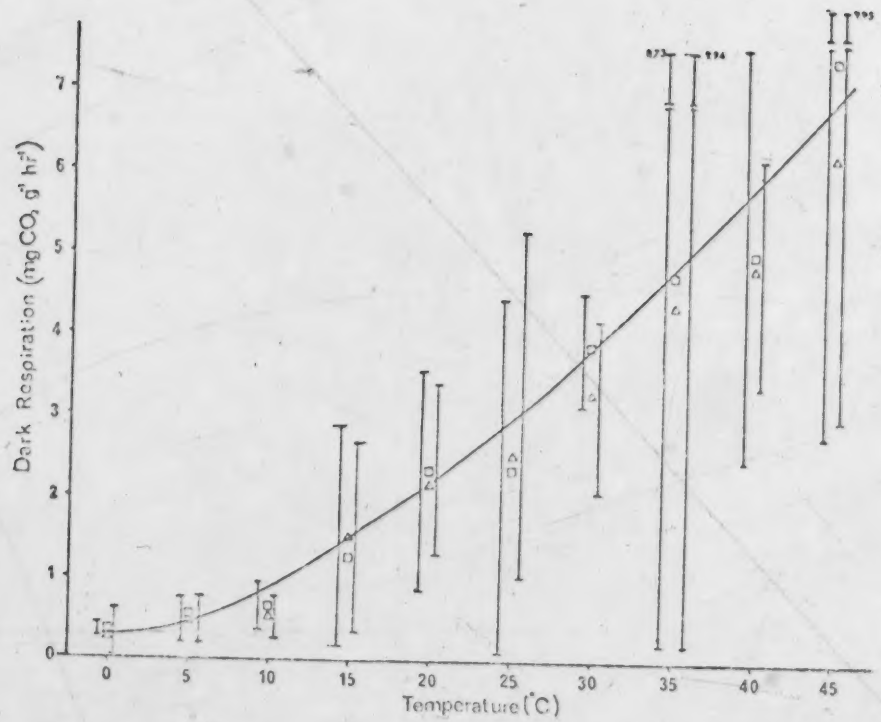
Table 6. Optimum temperature and average rates of net assimilation of various C_3 plants.

Plant	Temperature °C	Net Assimilation Rate		Reference
		mg CO_2 g^{-2} hr^{-1}	mg CO_2 dm^{-2} hr^{-1}	
Atriplex hastata	26°	9	30	Hofstra and Hesketh, 1969
Juniperus virginiana	20°	9		Ormsbee, et al., 1976
Diospyros virginiana	25°		17	Bacone, et al., 1976
Ulmus alata	25°		15	Bacone, et al., 1976
Encelia virginensis	25°	21		Mooney and West, 1964
Artemisia tridentata	20-25°	7		Mooney and West, 1964
Ambrosia artemisiifolia	20-25°		21	Bazzaz, 1974
Sassafras albidum	25-30°		11	Bazzaz, et al., 1972
Glycine max (soybean)	35°		20	Hofstra and Hesketh, 1969
Beta vulgaris (sugarbeet)	34°		28	Hofstra and Hesketh, 1969
Thalictrum alpinum polyploid	20°	24		Mooney and Johnson, 1965
Thalictrum alpinum diploid	20°	17		Mooney and Johnson, 1965
Viola adunca polyploid	20°	26	12	This Study
Viola adunca diploid	20°	23	11	This Study

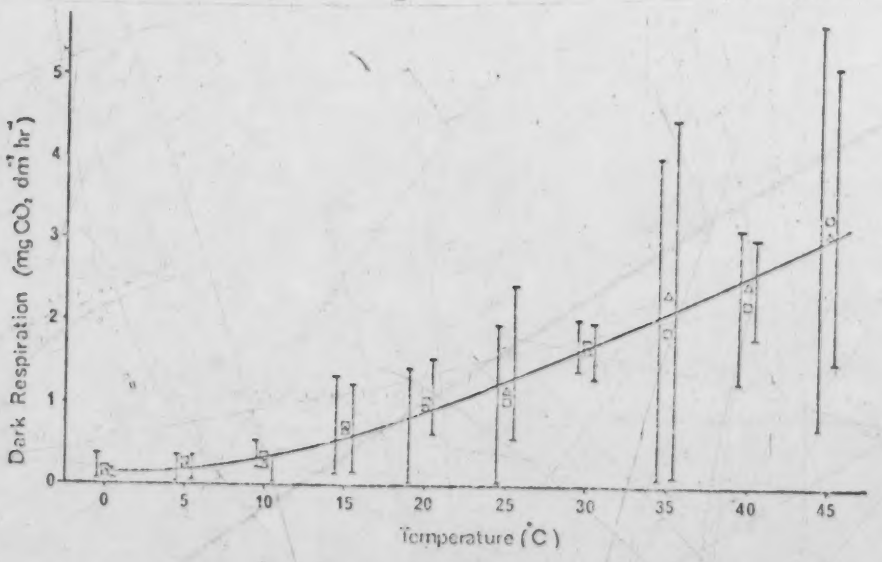
between ploidy levels are very small especially below leaf temperatures of 25° C (Figures 11a and 11b). At leaf temperatures above 25° C polyploid plants possess slightly greater dark respiration rates when expressed as mg CO_2 g^{-1} hr^{-1} (Figure 11a). When dark respiration is expressed as mg CO_2 dm^{-2} hr^{-1} however, these differences are reduced. For example, at leaf temperatures of 35° and 40° C it is the diploid plants which exhibit greater dark respiration rates (Figure 11b). This shows that differences between ploidy levels are inconsistent. Because no statistically significant differences in the dark respiration rates between ploidy levels exist, especially at low leaf temperatures, it is clear that polyploid plants are not any more efficient at carrying on metabolism than diploid plants. The only directly comparable results to these are those of Mooney and Johnson (1965) who found arctic triploid Thalictrum alpinum had slightly greater dark respiration rates than diploids at 20° C (see literature review, page 43). The rates of dark respiration of V. adunca are quite similar to the rates found in Diospyros virginiana, Ulmus alata, Artemisia tridentata and Antennaria rosea listed in Table 7 (page 54).

An Arrhenius plot of the dark respiration rates of the chromosome races in V. adunca is shown in Figure 12 (page 55). This plot substantiates the fact that differences between ploidy levels are small. No noticable inflection point in the slope of the Arrhenius plot is apparent at 10° C (Figure 12). Lyons (1972, 1973) examined mitochordical respiration of chilling sensitive and chilling resistant plants. A noticable inflection point occurred at 10° C in the slope of the Arrhenius plot in only those plants which are chilling sensitive. This information

coupled with the fact that V. adunca can carry on positive net assimilation at leaf temperatures of 0° C and colder, indicate that this plant is indeed chilling resistant. Similar findings were determined in Dryas integrifolia (Hartgerink, 1975).



a) Dark respiration on a mg CO_2 g^{-1} hr^{-1} basis vs. temperature.



b) Dark respiration on a mg CO_2 dm^{-2} hr^{-1} basis vs. temperature.

Figure 11. Response of dark respiration by single attached leaves of Viola adunca to temperature. Acclimation temperature 20°C. (□--3n and 4n plants, Δ--2n plants)

Table 7. Dark respiration rates of various C_3 species measured at 20° C.

Species	Rate mg CO_2 g^{-1} hr^{-1}	mg CO_2 dm^{-2} hr^{-1}	Reference
Dryas integrifolia	7.9		Hartgerink, 1975
Encelia virginesis	1.60		Mooney and West, 1964
Artemisia tridentata	1.4-2.10		Mooney and West, 1964
Happlopappus apargioides	1.50		Mooney and West, 1964
Diospyros virginiana		1.00	Bacone, et al., 1976
Ulmus alata		1.00	Bacone, et al., 1976
Ambrosia artemisiifolia		3.2	Bazzaz, 1974
Sassafras albidum		0.63	Bazzaz, et al., 1972
Populus tremuloides	3.77		Mooney and West, 1964
Pinus aristata	0.16		Mooney and West, 1964
Antennaria rosea	2.53		Mooney and West, 1964
Thalictrum alpinum 3n	5.6		Mooney and Johnson, 1965
Thalictrum alpinum 2n	4.5		Mooney and Johnson, 1965
Viola adunca polyploid	2.20	1.00	This Study
Viola adunca diploid	2.00	.95	This Study

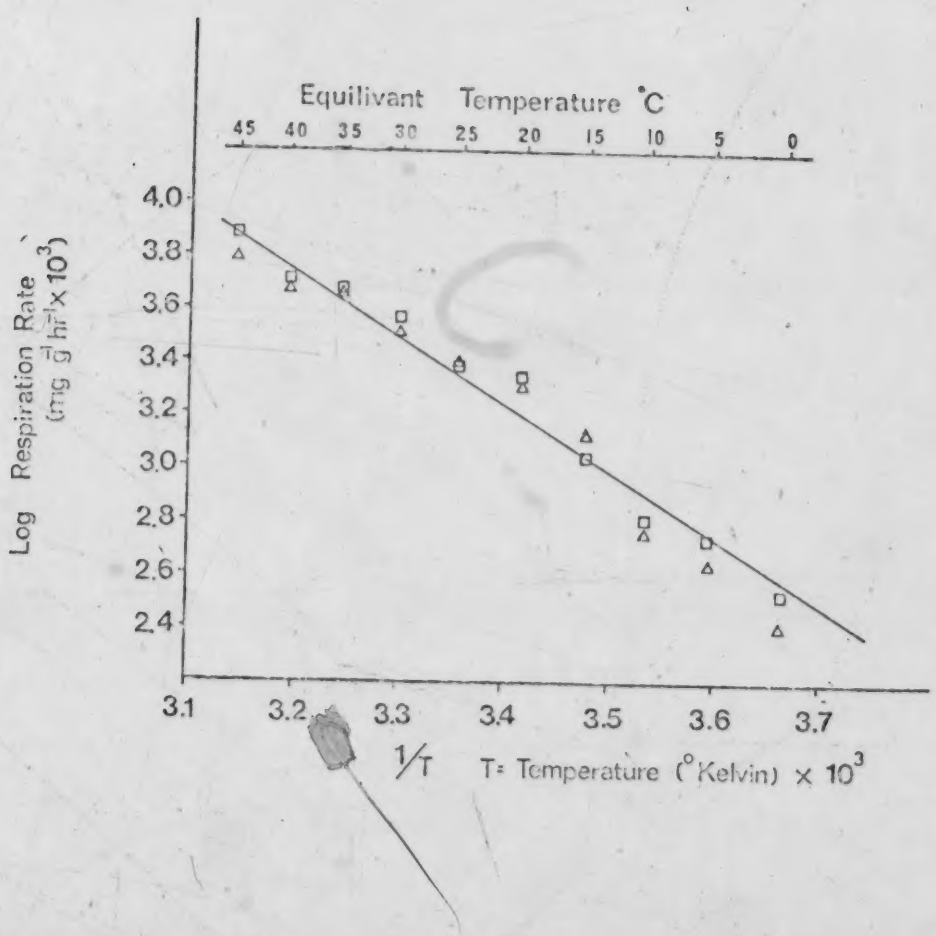


Figure 12. An Arrhenius plot of dark respiration (log mg CO_2 g^{-1} hr^{-1}) vs. temperature (1/absolute T °K). Acclimation temperature 20°C. (□--3n and 4n plants, △--2n plants)

WATER RELATIONS

Literature Review

Life has evolved in a medium of water and the content of water in plant tissues is usually high (80 to 90%) (Slatyer, 1967). Hsiao (1973) has stated rather concisely on the importance of water that, "the number of places where water plays a crucial role in the plant complex is astronomical."

To determine if polyploid Viola adunca plants are hardier than diploid plants under conditions of water stress, the two chromosome races (polyploid and diploid) were compared in terms of the following parameters which were measured as a function of desiccation: 1) water potential and its component potentials 2) relative water content 3) leaf resistance and 4) net assimilation.

In order to gain a more complete understanding of plant behavior both Hsiao (1973) and Courtin and Mayo (1975) have pointed out the importance of measuring both the water potential and its components. Unfortunately this has only been the practice recently. The species listed in Table 8 (page 57) show that agriculutral plant species tend to have higher water potentials than most native species. For many agriculutral species inhibition of net assimilation occurs at the maximum water potential given in Table 8 (also see Table 10, page 60). (Boyer, 1970b; Acedevo, Hsiao, and Henderson, 1971). Native species, in contrast, show inhibition of growth at lower maximum water potantials.

Table 8. Maximum and minimum water potential of various species.

Species	Water Potential in bars				Reference
	Maximum		Minimum		
	ψ	$\psi\pi + \psi_\gamma$	ψ	$\psi\pi + \psi_\gamma$	
Soybean	-2.5		-17		Teare and Kanemasu, 1972
Sunflower	-2	-8	-10	-10	Boyer and Potter, 1973
Corn	-7		-18		Turner, 1974
Cotton	-8	-12	-19	-19	Gardner and Ehlig, 1965
Ulmus alata	-2		-20		Bacone et al., 1976
Sassafras albidum	-8		-21		Bazzaz et al., 1972
Ambrosia artemiscifolia	-6		-21		Bazzaz, 1974
Dryas integrifolia	-7	-18	-50	-50	Hartgerink, 1975
Larrea divaricata		-25		-40	Oechel et al., 1972
*Viola adunca	-8	-15	-21	-21	This study

*Combined data for both ploidy levels.

Some xerophytic species of desert, arctic and alpine environments can even assimilate CO_2 at much lower water potentials (Table 10).

Höfler (1920) suggested that the pattern of change of the osmotic and turgor components of water potential is related to the relative cell volume (and therefore water content of the cells). The pattern of change of these two components could thus be related to the relative elasticity or rigidity of the cell walls. This theory stated that plant cells with more rigid cell walls would show a larger decrease in turgor pressure but with a small decrease in cell volume and in osmotic potential than those plant cells with more elastic cell walls. Those cells with more elastic cell walls would therefore exhibit a smaller decrease in turgor than cells with rigid walls. The occurrence of cell walls which are rigid is considered by Walter (1931, after Walter and Kreeb, 1970) to be a water conserving adaptation. Zavitkowski and Ferrel (1968) found that xerophytic ecotypes of Douglas fir did show larger decreases in turgor than the more mesic ecotypes and therefore had rigid cell walls. Hartgerink (1975) found however that Dryas integrifolia, a plant adapted to dry, well drained arctic beach ridges did not show large decreases in turgor and therefore had relatively elastic cell walls even though the plant is xerophytic in nature.

The response of net assimilation in the light during water stress is governed by the degree of stomatal opening which in turn regulates the leaf diffusive resistance to carbon dioxide (Hsiao, 1973). Leaf resistance values are species variable as shown in Table 9 (page 59). It is seen that agricultural species usually have a much lower minimum leaf resistance than those species native to xerophytic habitats (Levitt, 1972).

Table 9. Minimum and maximum leaf resistances to water loss measured on various plant groups and species.

Plant group or species	Leaf Resistance ($sec\ cm^{-1}$) Minimum	Maximum	Reference
Cultivated species	0.5 to 3	6 to 52	Holmgren et al., 1965; Ehrler and van Bavel, 1968; Al Ani and Beirhuizen, 1971; Biscoe, 1972
Deciduous species	1.2 to 20	21 to 58	Holmgren et al., 1965; Small, 1972; Davies and Kozlowski, 1974
Alpine herbs	0.8 to 1.6	4 to 11	Ehleringer and Miller, 1975
Arctic species	1 to 3	30 to 40	Stoner and Miller, 1975
Dryas integrifolia	5.6	24	Hartgerink, 1975
Pinus banksiana	8	300	Mayo pers. comm.
Viola adunca polyploid	3.4	17.5	This study
Viola adunca diploid	3.9	17.6	This study

Table 10. Water potentials of various species at maximum rates of net assimilation and 50% and 0% of the maximum rate.

Species	Water Potential (bars) 100%	50%	0%	Reference
Tomato	-6.5	-10	-14	Brix, 1962
Corn	-3.5	-13	-16	Boyer, 1970a
Soybean	-11	-16	-24	Boyer, 1970a
Sunflower	-8	-15	-18	Boyer, 1970b
Chilopsis	-1	-15	-35	Odening et al., 1974
Encelia	-1	-15	-46	Odening et al., 1974
Geum rossii	-7	-18	-28	Johnson et al., 1974
Kobresia	-12	-24		Johnson et al., 1974
Deschampsia	-9	-23	-38	Johnson et al., 1974
Larrea	-10	-27	-75	Odening et al., 1974
Artemesia			-92	Kappen et al., 1972
Dryas integrifolia	-9	*(-18)	*(-25)	Hartgerink, 1975
Sassafras albidum	-8	*(-17)	*(-21)	Bazzaz et al., 1972
Ulmus alata	-6	* -18	-20	Bacone et al., 1973
ΔViola adunca	-9	-18	-24	This study

Δ data combined for both ploidy levels

* projected values

The response of leaf resistance to desiccation usually follows a characteristic pattern. The leaf resistance remains constant until a threshold water potential is reached below which the resistance increases exponentially (Kanemasu and Tanner, 1969; Jordan and Ritchie, 1971; Beadle et al., 1973). This is explained by the fact that when the threshold water potential is reached the stomata close rapidly. During water stress, abscissic acid (ABA) concentrations are found to increase (Jones and Mansfield, 1970; Horton, 1971). It is also well known that exogenously applied ABA is a fast acting inhibitor of stomatal opening (Cummins, Kende and Raschke, 1971; Kriedemann et al., 1972). It is quite possible that stomatal opening and therefore leaf resistance is regulated by changes in the ABA concentration. But it is questionable whether the endogenous ABA can act fast enough to promote stomatal closure (Hsiao, 1973).

Other environmental parameters which control leaf resistance are leaf temperature, light and concentrations of both carbon dioxide and water in the atmosphere surrounding the leaf. For a complete discussion of these the reader is referred to Meidner and Mansfield (1965) and Hsiao (1973).

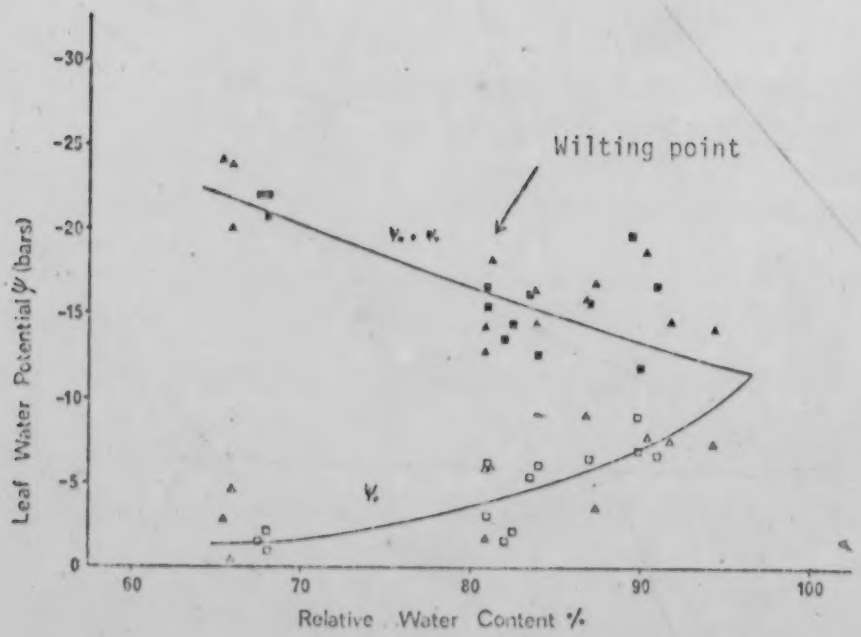
Although the response of net assimilation rates to decreasing water potential is most directly caused by hydro-active closure of stomata, Slavik (1965) points out other factors which can lead to reduced net assimilation rates. These factors mentioned briefly are: 1) cytoplasmic ultrastructural change affecting enzyme activity and; 2) dehydration of cuticle epidermal walls and cell membranes which reduce affinity for and permeability to CO_2 (Slavik, 1965).

Net assimilation response to water stress varies significantly with species as shown in Table 10. The net assimilation rates of agricultural species are usually more sensitive to decreases in water potential than native species. Ecotypes of Tsuga canadensis were found to have different responses of net assimilation to water stress (Eickmeier, Adams and Lester, 1975). Populations from southern seed sources had higher minimum leaf resistance values than northern populations when experiencing no water stress. This factor allowed for greater rates of net assimilation under water stress than for northern populations studied.

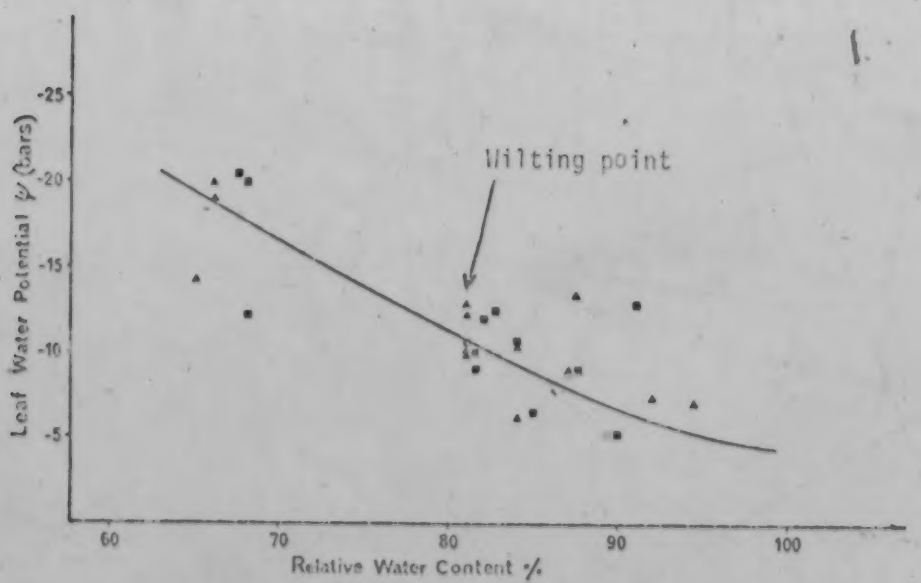
Results and Discussion

The average water potential for well-watered polyploid and diploid Viola adunca is -7.9 bars at 20° C. Under these conditions the water potential of diploid plants ranged from -6.2 bars to -10.4 bars while polyploid plant values ranged from -5.3 to -10.66 bars. There are no significant differences associated with ploidy. These water potential values are lower than most agricultural species cited in the literature but are similar to the native species listed in Table 8 (page 57).

The response pattern of water potential and its components to relative water content is shown in Figure 13 (page 63). It can be seen by the close point distribution in Figure 13a and 13b that no discernible differences between ploidy levels exist. Diploid plants do seem to have lower relative water content values when the leaves were wilted (Figure 13a). These values are not significantly large (only a difference of 3%) and could be due to chance. For both ploidy levels there is a sharp decrease in the osmotic potential relative to a gradually decreasing turgor potential from 90 to 80% relative water content.



a) Component potentials: osmotic and matric ($\psi_\pi + \psi_\gamma$) and turgor (ψ_p). (■ and □--3n and 4n plants, ▲ and △--2n plants)



b) Total water potential ψ vs relative water content. (■ --3n and 4n plants, ▲--2n plants)

Figure 13. Leaf water potential of the chromosome races in Viola adunca as related to changes in leaf relative water content at 20° C.

Both osmotic and turgor components decrease in the same fashion relative to decreasing relative water content and suggest that V. adunca possesses cell wals which are rigid. This property of the cell walls therefore suggest that V. adunca is xerophytic in nature. Since V. adunca grows on well drained exposed slopes (personal observation) the occurrence of rigid cell walls may be an adaptation it needs to survive in times of moisture stress. This observation would tend to support Höfler's (1920) theory that xerophytic species must have rigid cell walls (literature review-page 58).

The response of turgor to relative water content is shown in Figure 13a. It can be seen that turgor remains fairly stable between 90 to 80% relative water content, but below 80% at an osmotic potential of -15 bars turgor decreases at a uniform rate until the relative water content reaches 65%, the point at which the leaves wilt. Therefore V. adunca exhibits a two-phase response of osmotic potential to relative water content, but not in the same manner described by Gardner and Ehlig (1965) or Hartgerink (1975) who both found that osmotic potential decreases sharply at relative water contents slightly below full turgidity but that further decreases were not as dramatic.

The mean minimum leaf resistance to water loss at 20° C for non-stressed polyploid V. adunca is 3.4 sec cm^{-1} and for diploid plants 3.9 sec cm^{-1}. These differences are not sufficiently large and could be due to chance. If polyploid plants were at all hardier than diploid plants it is possible that they would show a higher minimum leaf resistance. The minimum leaf resistance values of V. adunca are slightly higher than values measured for agricultural species and alpine herbs listed in Table 9 (page 59).

The response of leaf resistance to decreasing water potential of V. adunca is seen in Figure 14 (page 66). No significant differences in the leaf resistance response are seen indicating that they respond similarly to water stress. The leaf resistance values of both ploidy levels decrease gradually below water potential of -8 bars until a threshold water potential is reached (-14 bars) below which leaf resistance values decrease exponentially. A similar type of response has been observed with both agricultural and native species (literature review, page 61). The threshold water potential value is similar to that observed in cotton (-16 bars) (Jordan and Ritchie, 1971) in snapbean (-14 bars) (Kanemasu and Tanner, 1969) and sorghum (-14 bars) (Beadle et al., 1973).

The influence of leaf water potential on leaf resistance to water vapor loss and on net assimilation is shown in Figure 15 (page 67). As can be seen by the scattered points in the plot there are no significant differences between ploidy levels. Since mean water potential and leaf resistance values under non-stressed conditions are almost identical it is reasonable that they would respond similarly under conditions of water stress. This infers that polyploid plants have no greater hardiness than diploid plants.

It is interesting that optimum net assimilation rates are at water potentials less than full hydration (Figure 15). This observation may be explained by the fact that at full turgidity (water potential -6.5 bars) guard cell aperature opening is probably less than at a few bars below full turgidity (-9 bars) (Brix, 1962). Therefore at full turgidity less efficient gas exchange can take place since the guard cells are not as

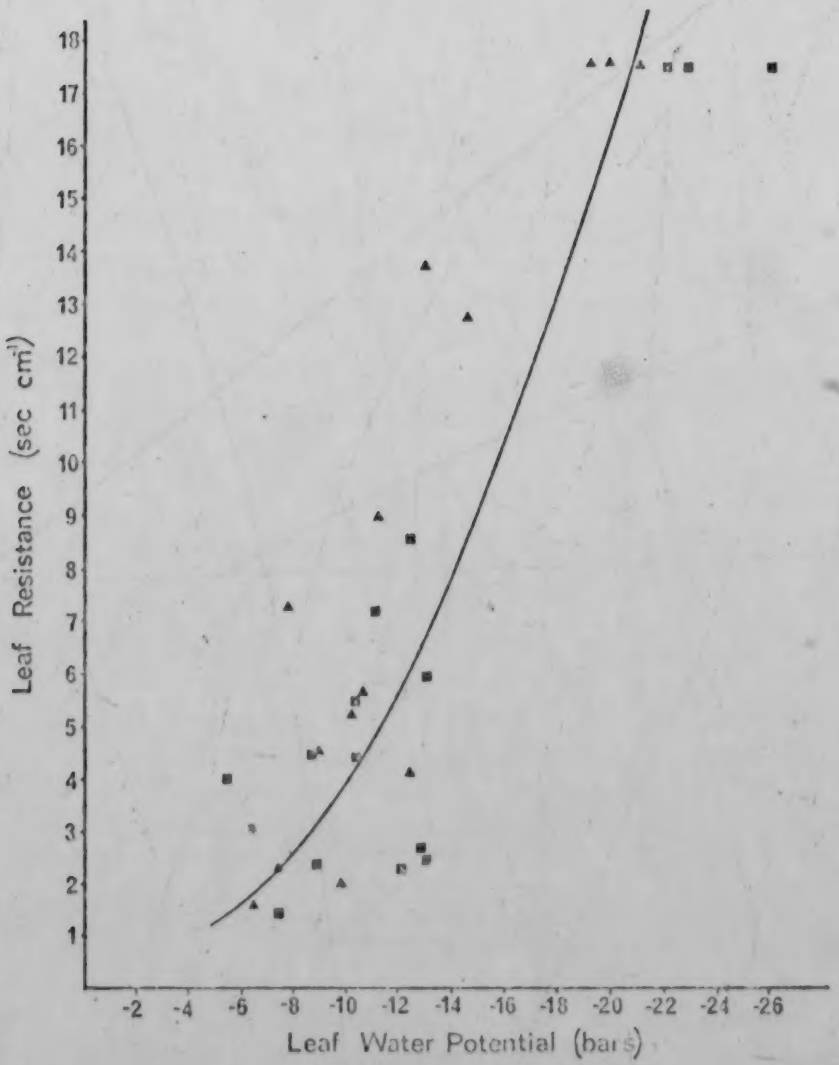


Figure 14. The influence of leaf water potential of the chromosome races in Viola adunca on leaf resistance to water vapor loss. Light: 200 μEm^{-2} sec^{-1}; leaf temperature: 20° C; relative humidity: 75 to 80%. Leaf resistance was determined on both abaxial and adaxial surfaces. (■ --3n and 4n plants, ▲--2n plants)

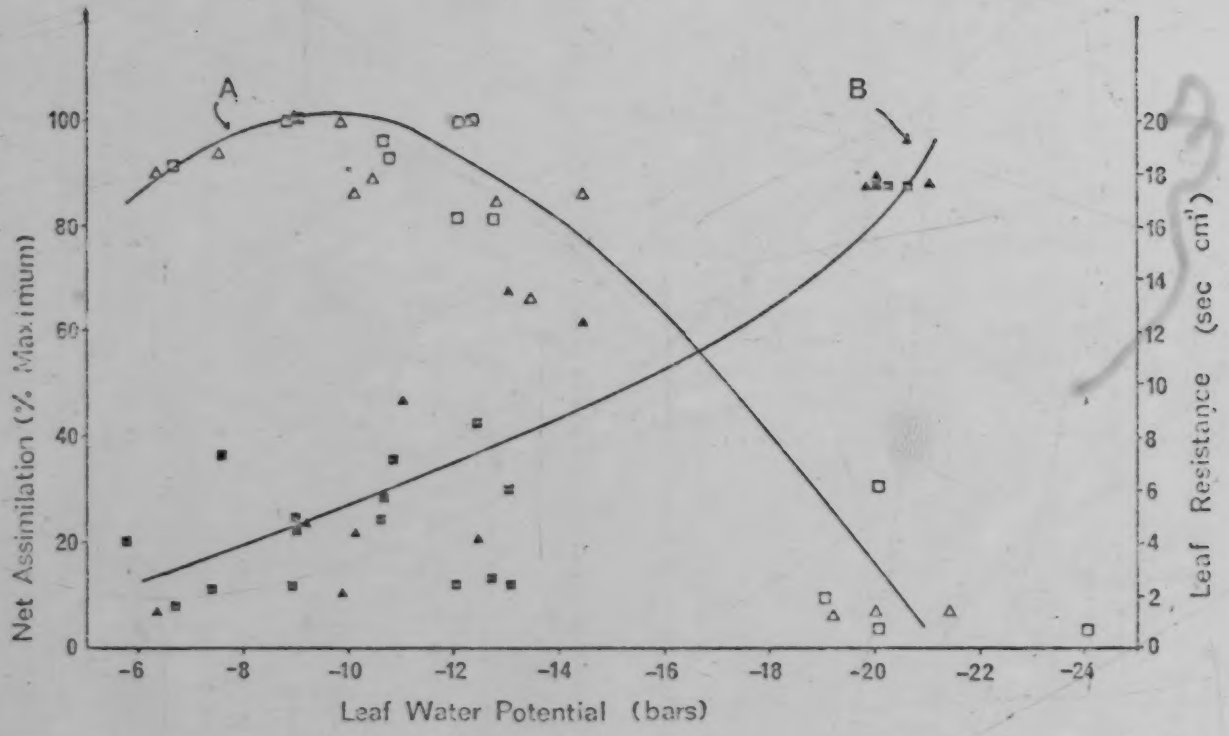


Figure 15. The relationship of net assimilation (A) and leaf resistance (B) of the chromosome races in Viola adunca to leaf water potential. The data was collected from 3 plants of each ploidy level over a 6 day drying period. Water potential and leaf resistance were measured on adjacent leaves. Light: 500 μEm^{-2} sec^{-1}; Leaf temperature 20° C; relative humidity 75 to 80%. (□ --3n and 4n plants, △--2n plants)

fully open. This same observation in net assimilation response to water potential was observed in tomato (Brix, 1962) and in Dryas integrifolia (Hartgerink, 1975).

The response of net assimilation to water potential in V. adunca is similar to many of the species listed in Table 10 (page 60). It is interesting to find that V. adunca still fixes carbon dioxide positively down to a water potential of -24 bars. This can probably be explained by cuticular gas exchange taking place and not a function of stomatal gas exchange. The water potential at which net assimilation rates decrease dramatically is very close to -14 bars (Figure 15, page 67). Since -14 bars water potential is the threshold below which leaf resistance values increase, this suggests that net assimilation rate responses to decreasing water potential are controlled primarily through leaf resistance and therefore through stomatal response. The threshold water potential of leaf resistance and net assimilation can furthermore be correlated with the behavior of relative water content and the leaves wilting point. Figure 13b shows that below -12 bars water potential (RWC 80%), the relative water content dropped off quickly and leaf wilting occurred (see page 63). Furthermore, relative water content was not measurable until a water potential of about -21 bars was reached and the relative water content dropped to 65%.

The conclusion of the water relations studies is that ploidy per se makes no difference in the response of Viola to increasing moisture stress.

CONCLUSIONS

The chromosome races in Viola adunca are unevenly distributed in North America; tetraploid plants are found growing further north and diploids generally have a more southerly distribution. Similar distributional patterns have been described for chromosome races of other species (Cain, 1944). The presence of all three known chromosome races of V. adunca (including a triploid) growing naturally in the Cypress Hills, Alberta afforded a good opportunity to determine if polyploid plants are any different physiologically and if they are more tolerant of environmental stress conditions (or hardier) than diploid plants.

The responses of net assimilation rates to light intensity are quite similar in both ploidy levels (Figures 2 through 6). The light compensation and saturation points and ½ maximum saturation values are nearly identical. The light compensation points are very low (18 μEm^{-2} sec^{-1}) at 0° C and rise rapidly at temperatures above 10° C. The light saturation point of both ploidy levels at 20° C was ca. 400 μEm^{-2} sec^{-1}. This indicates that V. adunca is able to utilize effectively a wide range of light levels, i.e., it has a low light compensation point and relatively high saturation values.

There were no statistically significant differences in the temperature response of either net assimilation or dark respiration. The optimum temperature for CO_2 assimilation for both ploidy levels was 20° C. The maximum net assimilation rate for polyploid plants was

26 mg CO_2 g^{-1} hr^{-1} (12 mg CO_2 dm^{-2} hr^{-1}) and for diploid 23 mg CO_2 g^{-1} hr^{-1} (11 mg CO_2 dm^{-2} hr^{-1}). Net assimilation and dark respiration rates at extremely low temperatures (0° C) and high temperatures (45° C) are very similar. The ability of these plants to carry on photosynthesis and respiration under these temperature extremes could be advantageous for plant survival in an area such as the Cypress Hills where spring-time temperatures can fluctuate dramatically in a short period of time. The similarity of responses of the chromosome races indicates that polyploid plants are not hardier than diploid plants, at least with respect to the parameters studied.

There are no statistically significant differences in the ability of either ploidy level to withstand moisture stress. The mean water potential for both plants is -7.9 bars at 90% relative water content (full turgidity). The maximum net assimilation rates of both ploidy levels are not attained until a water potential of ca., -9 bars is reached (Figure 15). Leaf resistance and net assimilation response to desiccation show that these two parameters have the same threshold water potential, (-14 bars), which indicates that stomatal closure is the primary reason for decreases in the net assimilation rates.

Since few differences in physiological responses are apparent, especially under conditions of temeprature and water stress, it is concluded the polyploidy in Viola adunca does not confer any greater ability to withstand environmental extremes. The different ploidy levels exhibit similar rates of net assimilation and dark respiration over a wide range of light, temperature and moisture regimes.

This study does not however rule out the possibility that polyploidy confers some advantage such as seedling survival which could explain the observed distribution patterns of chromosome races. It does show that polyploidy *per se* does not seem to influence the measured physiologic parameters. This study suggests that ploidy *per se* may not be as important as heretofore believed. However, more work is necessary to fully understand the effects of polyploidy.

Studies of other species are desirable and are known to be under way. Betsy Flint at Duke is currently studying the effects of polyploidy in *Epilobium augustifolium* (pers. comm.). Studies on seedling survival under environmental extremes are necessary. Studies using chromosome races from different geographic locations are necessary. Only after further physiologic work along the lines described above can the question of the influence of ploidy be fully elucidated.

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APPENDIX A

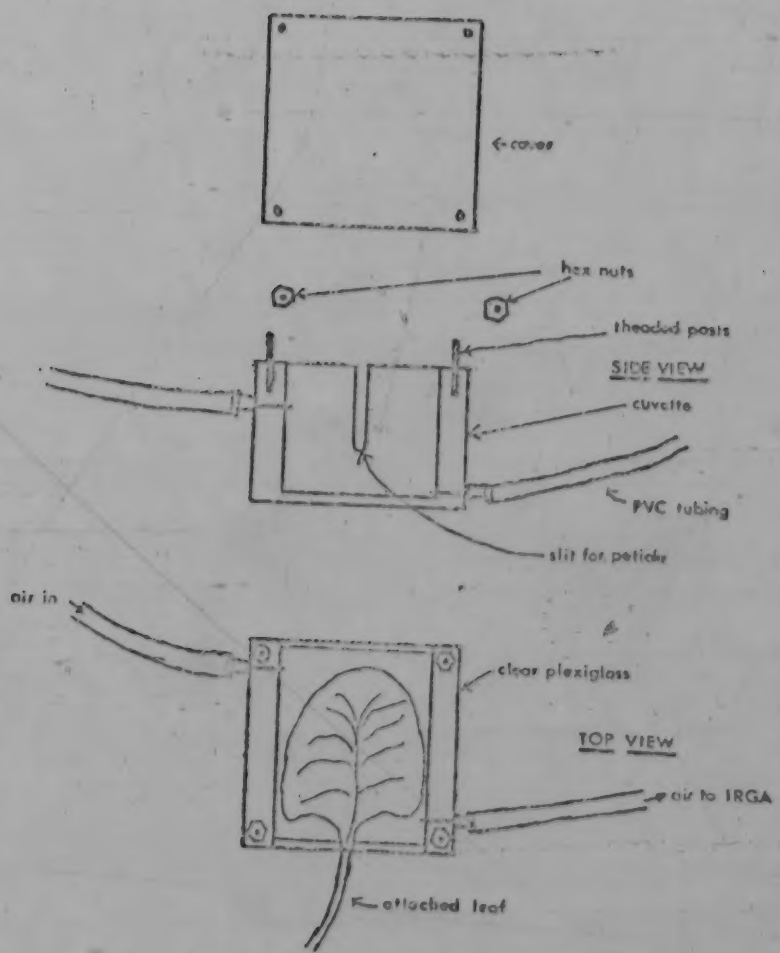

Figure 16. Diagram of the cuvette used to measure net assimilation by single leaves of Viola adunca.

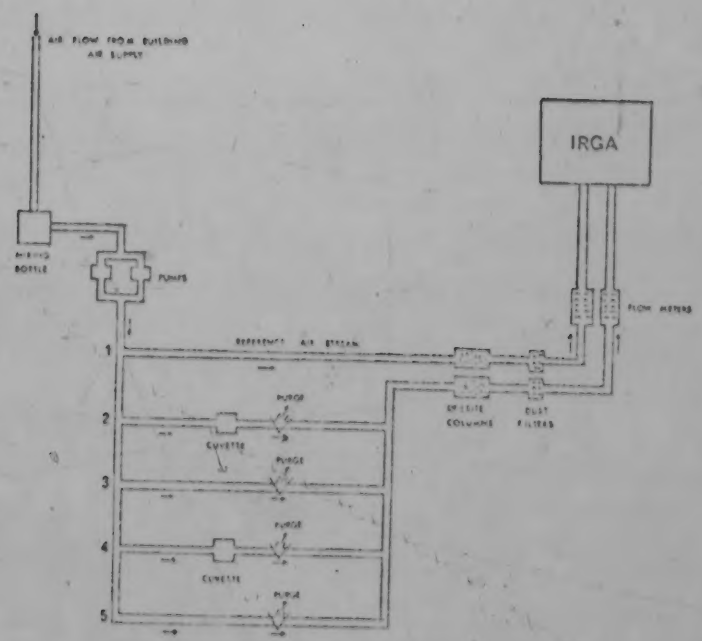

Figure 17. The flow diagram of the gas analysis system used for measuring net CO_2 exchange of leaves from two different ploidy levels. Attached leaves are inserted in the cuvettes. The flow of air to the IRGA is altered from sample air streams 2 or 4, and the reference air streams, 3 or 5, by the use of 3 way solenoid switches. In both cases, air flows through reference air stream 1.

APPENDIX B

An ISCO spectroradiometer analysis of light quality by various sources of illumination used during the experiments.

Wavelength (nm)	Intensity of irradiance ($\mu W \cdot cm^{-2} \cdot nm^{-1}$)		
	Mercury vapor lamp at 8"	High intensity growth chamber* at 12"	Quartz-iodide at 12"
380	9.9	2.0	2.5
400	33.1	22.0	13.2
425	17.7	24.6	18.6
450	19.5	30.0	23.3
475	4.73	33.1	27.9
500	5.9	44.9	31.7
525	7.2	24.0	37.7
550	166.3	69.0	54.7
575	148.0	172.0	63.6
600	13.0	21.6	68.8
625	29.1	93.7	72.0
650	52.2	41.2	75.0
675	42.8	39.9	78.1
700	16.0	21.6	85.7
725	7.6	18.8	87.4
750	8.1	20.5	96.0
800	4.2	54.7	106.3
850	4.8	67.9	109.3
900	4.5	14.4	104.8
950	5.7	14.3	107.1
1000	23.3	13.9	103.3
1050	15.4	12.3	106.4
1100	6.5	11.3	88.5
1150	16.1	19.3	86.7
1200	8.1	5.9	75.3
1250	5.8	6.9	67.6
1300	5.0	7.8	62.7
1350	8.75	3.7	59.5
1400	12.6	3.6	54.0
1450	4.76	2.6	47.6
1500	5.5	3.2	43.9
1550	6.76	2.94	39.7

* combined lucalux, metalarc and incandescent lamps